

An Unprecedented Outbreak of Rice Blast on a Newly Released Cultivar BRS Colosso in Brazil

Anne S. Prabhu, M. Cristina Filippi, Gisele B. Silva, Valácia L. Silva Lobo and Orlando P. Morais

Abstract Rice blast occurred in epidemic proportions on a newly released upland rice cultivar BRS Colosso, in the rice growing season 2004/2005. Twenty isolates were collected from the affected panicles of the cultivar BRS Colosso from three different States, two pathotypes IB-1 and IB-17 were identified. They were classified into thirteen Brazilian pathotypes based on the reaction pattern on eight upland rice cultivars, utilized as local differentials. Differences in aggressiveness of the isolates on the cultivar BRS Colosso were evident. Ten highly aggressive isolates were used to determine the partial resistance to leaf blast in the BRS Colosso and BRS Bonança. There was no significant isolate x cultivar interaction for partial resistance. The mean leaf blast severity was significantly higher in BRS Colosso than in BRS Bonança. Inoculation of culms with the same ten isolates showed cultivar x isolate interaction. Some isolates were more aggressive showing severe culm blast. There was no correlation among the aggressiveness of the isolates on leaf and culm. The disease outbreak in BRS Colosso could be attributed to the absence of adequate degree of partial resistance, the preexistence of compatible pathotypes IB-1 and IB-17 and their dissemination through seed.

Keywords Epidemiology · *Magnaporthe oryzae* · Partial resistance

1 Introduction

An unprecedented rice blast outbreak caused by *Magnaporthe oryzae* [(Hebert Yaegashi & Udagawa)] (Couch and Kohn 2002) [anamorph *Pyricularia grisea* (Cooke) Saccardo] has been reported in the rice growing season 2004/2005, in different commercial farms of a newly released cultivar BRS Colosso, by rice producers and confirmed by various research scientists and extension agents during their visits. The upland rice cultivar BRS Colosso developed for superior long grain

A.S. Prabhu (✉)

Embrapa Rice and Beans, Caixa Postal 179, CEP 75375-000, Santo Antônio de Goiás, GO, Brazil
e-mail: prabhu@cnpaf.embrapa.br

quality and high yield potential was released for cultivation during 2003/2004 growing season. It was grown in extensive areas in the States of Minas Gerais, Goiás, Tocantins and Mato Grosso. The losses were found to be high and some farmers could not even harvest a single bag of rice. It is difficult to define the point at which an outbreak of a disease can be considered an epidemic. The widely cited disease epidemics such as coffee rust, maize rust, soybean rust are those which were destructive covering large areas in a short period of time. There are several epidemics which are local due to differences in climatic, topography and soil conditions. It is not necessary that all epidemics cover large areas but there may be destructive outbreaks over limited areas or limited to one cultivar. The only common factor is the destructiveness and loss in grain yield, but there is no numerical threshold or value at which an outbreak deemed to become an epidemic (Tarr 1972).

The affected plants showed typical blast symptoms on internodes and nodes as well as neck and panicle blast. The widespread occurrence of nodal blast in the upland rice may be considered as the first report even though it is commonly observed in irrigated rice. The panicle blast could not be controlled even with two applications of a systemic fungicide. The destructive nature of rice blast has been known world wide (Ou 1985) but the total grain yield losses even in the first year of release of this new cultivar lead to different speculations as to its cause. It was attributed to high blast susceptibility of the cultivar, intensive cultivation using heavy doses of nitrogen fertilizer, late application of nitrogen top dressing, favorable weather conditions, drought stress before or soon after panicle emergence, occurrence of a new race of pathogen or a high frequency of the preexisting matching races to the resistance genes of this cultivar, vertifolia effect due to lack of partial resistance, seed-borne infection, the resistance of the pathogen to the widely used fungicide tricyclazole.

Other cultivars, such as BRS Primavera and BRS Bonança, in the same farm or neighboring rice farms were found to be affected, but did not cause as colossal yield losses. Because of this observation the weather factor favorable to the occurrence of disease in epidemic proportion was ruled out. The cultivar has been tested in yield trials and blast nursery over a period of three years before its release. The examination of disease scores in the field trials showed that the panicle blast scores were low or similar to the susceptible checks. The mean leaf blast rating in blast nursery was 3.5 with a score ranging 0–5 in eight different test sites, whereas the susceptible cultivar Primavera showed mean score of 4.5 and 0–9 range. The data showed that the cultivar BRS Colosso exhibited susceptible reaction for leaf blast in tests before its release, but did not fully explain the sudden blast outbreak of this cultivar in the first year of its release. In general, the blast susceptibility of a given cultivar increases with an increase in area cultivated as a result of increase of a certain pathotype (Kiyosawa and Shiyomi 1976) in a stepwise manner. The short lived nature of varietal resistance is commonly attributed to mutations that change the phenotype of a strain from avirulence to virulence, sexual recombination, asexual recombination, acreage of resistant varieties, genetic uniformity of varieties and low field resistance (Kiyosawa 1982; Valent and Chumley 1994) and the failure of breeding lines to encounter low frequency compatible pathotypes in a population

(Correa-Victoria and Zeigler 1993) The widespread occurrence of rice blast on BRS Colosso, a year after its release required investigations as to the cause of the disease outbreak in order to adopt appropriate measures in the release of improved cultivars in future.

The present investigation reports the occurrence of blast disease outbreak on a newly released cultivar, the identification of pathotypes collected from the infected panicles of rice cultivar BRS Colosso from three States and the degree of partial resistance of the BRS Colosso in relation to the cultivar BRS Bonança.

2 Material and Methods

Single conidial isolates of *M. oryzae* were obtained from sporulating lesions on panicle branches of improved upland rice cultivar, BRS Colosso. Diseased samples were collected from farmers and experimental fields during two consecutive years for establishing isolates. Twenty isolates obtained from affected panicles were tested for identification of pathotypes and aggressiveness of the virulent isolates.

Pathotypes were identified based on the reaction pattern on eight standard international differential cultivars (Dular, Kanto 51, NP125, Raminad Str 3, Usen, Zenith, Caloro and Sha-tiao-tsao) using the standard procedure (Atkins et al. 1967; Ling and Ou 1969) and eight Brazilian differential cultivars (Carajás, Confiança, Maravilha, Primavera, Progresso, Caiapó, IAC 47 and IAC 201) according to Prabhu et al. (2002a). Plant materials for tests were planted in plastic trays (15 × 30 cm) containing 3 kg of soil and fertilized with NPK (5 g of 5-30-15 + Zn and 3 g of ammonium sulfate per 3 kg of soil). Eight standard international and eight Brazilian differential cultivars were sown, in 5.0 cm long rows, in one tray for identifying pathotypes of the test isolates. Leaf blast reaction was assessed at seven to nine days after inoculation taking into consideration only two types of reaction of the host, compatible or susceptible and incompatible or resistant reaction. To determine the partial resistance, the cultivars BRS Colosso (Kay Bonnet/CNA 7119) and BRS Bonança (CT7244-9-2-1-52-1/CT7232-5-3-7-2-1P//CT6196-33-11-1-3-AP) were seeded in separate trays, in eight 10 cm long rows per tray.

Initially differences in aggressiveness among the isolates of *M. oryzae* were determined based on inoculation of BRS Colosso using 20 isolates and two replications. In another experiment the partial resistance in cultivars BRS Colosso and BRS Bonança was studied with 10 of 20 aggressive isolates using a split plot design with two replications. The main plots consisted of isolates and the subplots cultivars, in total two trays per isolate and replication. Inoculations were done on 21-day-old plants with spore suspension (3×10^5 conidia/mL) in greenhouse as described earlier by Araújo et al. (2005). A tray containing international differential cultivars as a non-inoculated control was maintained to ensure that no contamination occurred during the inoculation procedure. Inoculations were repeated twice and the one that gave consistent reaction was used for pathotype determination.

The percentage of leaf area infected was measured at nine days after inoculation, using a 10 grade visual rating scale, based on percentage of leaf area affected according to Nottoghem (1981). A sample of 25 plants per replicate selected at random and the top fully opened leaf per plant was used for leaf blast assessment. For the variance analysis the disease severity data were transformed to $\arcsin \sqrt{x}$.

For determining the partial resistance to culm blast of the cultivar BRS Colosso in relation to the cultivar BRS Bonança, the two cultivars were seeded in plastic pots containing 5 kg of soil fertilized with NPK in greenhouse. A completely randomized block design with three replications was used. Inoculations were done using the injection method with ten isolates of pathotypes IB-1 and IB-17. Inoculations were done soon after panicle emergence when the distance between the collar of the flag leaf and panicle base was approximately 3–4 cm length. Spore suspension (0.05 ml/culm) was injected into the uppermost internode 2.0 cm below the panicle base. Three tillers/plant in total of nine tillers in 3 replications were inoculated. Disease assessment was done at twelve days after the inoculation of culms with spore suspension. Lesion size from the point of inoculation was used as criterion for assessing partial resistance because of the differences in spikelet sterility among inoculated tillers within the same plant.

3 Results and Discussion

Initial inoculation tests with 20 isolates collected from the affected panicles of the cultivar BRS Colosso showed differential interaction for resistance to leaf blast. However, all isolates showed susceptible reaction on BRS Colosso and the cultivar Liderança which was developed from its sister line of the same cross. None of the test cultivars showed resistance to all isolates (Table 1). Out of 20 isolates of *M. oryzae* collected from BRS Colosso during the epidemic year 2005 and the following year 2006, 14 were identified as belonging to pathotype IB-1 and six as IB-17 based on the reaction pattern of eight international differentials (Table 2). These pathotypes were found to be distributed independent of collection site, State and year of collection. The predominance of the pathotypes IB-1 was also reported in earlier tests conducted during 1986–88, among isolates retrieved from upland rice cultivars (Prabhu et al. 2002a). The pathotype IB-17 was reported to occur in the cultivar Liderança (CNAs 8983) in a previous investigation (Prabhu et al. 2003). New races of the pathogen may be introduced from elsewhere through seed or long distance dissemination of spores by wind. Sometimes the appearance of a new race with new parasitic potentialities through variation producing mechanisms such as genetic mutation and parasexuality may result in disease in epidemic proportions. The destructiveness may be enhanced by widespread cultivation of a susceptible cultivar which has not previously encountered the particular race present in the area. The results showed that these pathotypes were pre-existing and IB-1 was one of the predominant pathotypes on upland cultivars. Occasionally, a preexisting race or pathotype in low frequency increases in high proportion with the release of a new cultivar. The rice blast outbreak on irrigated rice cultivar Epagri 108 and

Table 1 Reaction of 12 commercial upland rice cultivars to *Magnaporthe oryzae* isolates retrieved from BRS Colosso

| Isolate | Upland rice cultivars | | | | | | | | | | | |
|---------|-----------------------|---|----------------|---|---|---|---|---|---|----|----|----|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 |
| Py-8762 | R ¹ | R | S ² | S | R | R | S | S | R | R | S | S |
| Py-8767 | R | S | S | S | R | S | S | S | R | S | S | R |
| Py-8769 | R | S | S | S | R | S | S | S | R | S | R | S |
| Py-8770 | R | R | R | R | R | S | S | S | R | S | S | S |
| Py-8784 | R | S | S | S | R | R | S | S | S | S | S | S |
| Py-8788 | R | R | S | R | R | R | S | S | S | S | S | S |
| Py-8790 | R | S | S | S | R | S | S | S | R | S | S | S |
| Py-8793 | R | R | R | R | R | R | S | S | R | R | S | S |
| Py-8794 | R | S | S | S | R | R | S | S | R | R | S | R |
| Py-8796 | R | S | S | R | R | R | S | S | S | R | R | R |
| Py-8797 | R | R | S | R | R | S | S | S | R | S | S | R |
| Py-8798 | R | R | S | S | R | S | S | S | R | S | S | S |
| Py-8803 | R | S | S | S | R | S | S | S | R | R | S | R |
| Py-8806 | R | R | S | S | R | R | S | S | R | S | S | S |
| Py-8807 | R | R | R | R | R | R | S | S | R | S | S | S |
| Py-8812 | S | S | S | S | S | R | S | S | R | S | S | S |
| Py-8815 | R | R | S | S | R | R | S | S | R | S | S | S |
| Py-8816 | R | S | S | S | R | S | S | S | R | S | S | R |
| Py-8818 | R | R | S | R | R | S | S | S | R | S | S | R |
| Py-8821 | R | S | S | S | R | R | S | S | S | S | S | S |

¹ 1-Carajás; 2-Confiança; 3- Maravilha; 4-Primavera; 5-Caiapó; 6-Progresso; 7-Colosso; 8-Liderança; 9- Curinga; 10-Conai; 11-Vencedora, 12-Bonaça.

² R = Resistant; S = Susceptible

109, one year after their introduction in the State of Tocantins was attributed to the increase of pathotype IB-45, which was possibly existing in a low frequency (Prabhu et al. 2002b). One of the possible explanations for the high frequency of pathotypes IB-1 and IB-17 in different and distant localities can be attributed to the primary source of inoculum originating from the infected seed. The basic seed was multiplied originally by three seed producers, in three different localities in the State of Mato Grosso during 2003/2004 rice growing season. Three hundred and thirty eight tons of seed, produced in an area in total 190 hectares was sold for planting about 5000.00 hectares in the following year 2004/2005. Comparison of pathotypes collected during the epidemic year and the succeeding year showed similar distribution pattern.

Thirteen pathotypes were identified based on Brazilian differential cultivars in contrast to two international pathotypes IB-1 and IB-17. They represented two race groups BB and BC. The differential cultivars Maravilha, Primavera, Progresso, IAC 201, Confiança, IAC 47 and Caiapó in descending order showed susceptible reaction to the large number of isolates tested. None of the 20 isolates of *M. oryzae* obtained from BRS Colosso were compatible to the differential cultivar Carajás. The reaction pattern on local Brazilian differentials furnish information on resistance gene frequencies that are useful for breeding purpose.

The analysis of variance of the data on percentage leaf area affected, in inoculation test of cultivar BRS Colosso with 20 isolates, showed significant differences

Table 2 Isolates of *Magnaporthe oryzae* collected from affected panicles of the cultivar BRS Colosso, pathotypes and percentage leaf area of cultivar BRS Colosso in greenhouse inoculation tests

| Isolate ¹ | Collectionsite/State | IP ² | BP ³ | Diseased leaf area (%) |
|---|----------------------|-----------------|-----------------|------------------------|
| Py 9057-P1 ¹ -06* ⁵ | Faz.Capivara/GO | IB-1 | BB-16 | 59.82 a ⁴ |
| Py 8790-P2 ¹ -05* | São Bernardo/GO | IB-1 | BB-2 | 52.70 a |
| Py 9056-P4 ¹ -06* | Lagoade Confusão/TO | IB-1 | BB-8 | 52.56 a |
| Py 8806-P3 ¹ -05* | Piu/TO | IB-1 | BC-16 | 52.20 a |
| Py 9061-P2 ¹ -06* | Faz.Capivara/GO | IB-17 | BC-7 | 49.90 ab |
| Py 8766-P2 ¹ -05* | Agua Boa/MT | IB-1 | BB-7 | 49.26 ab |
| Py 9063-P4 ¹ -06* | Faz.Capivara/GO | IB-17 | BC-7 | 48.12 ab |
| Py 8800-P2 ¹ -05* | Uruana/GO | IB-1 | BC-5 | 47.16 ab |
| Py 9052-P1 ¹ -06* | Lagoa de Confusão/TO | IB-1 | BB-7 | 46.72 ab |
| Py 9053-P2 ¹ -06* | Lagoa de Confusão/TO | IB-1 | BB-8 | 41.95 abc |
| Py 9059-P3 ¹ -06 | Faz.Capivara/GO | IB-17 | BC-32 | 34.10 abcd |
| Py 8813-P2 ³ -05 | Faz.Capivara/GO | IB-1 | BB-5 | 34.00 abcd |
| Py 8812-P1 ² -05 | Faz.Capivara/GO | IB-17 | BC-7 | 27.84 abcd |
| Py 8804-P2 ¹ -05 | Piu/TO | IB-17 | BC-16 | 27.74 abcd |
| Py 8793-P3 ¹ -05 | São Bernardo/GO | IB-1 | BB-7 | 26.55 abcd |
| Py 8762-P1 ¹ -05 | Agua Boa/MT | IB-1 | BB-1 | 25.06 abcd |
| Py 8811-P1 ¹ -05 | Faz.Capivara/GO | IB-17 | BC-6 | 20.70 abcd |
| Py 9068-P1 ¹ -06 | Faz.Capivara/GO | IB-1 | BB-13 | 5.09 bcd |
| Py 8770-P1 ¹ -05 | Agua Boa/MT | IB-1 | BB-16 | 2.15 cd |
| Py 8789-P1 ¹ -05 | São Bernardo/GO | IB-1 | BC-24 | 0.78 d |

¹ Py refers to *P. grisea* is followed by accession number of culture collection (Mycotec), *P* indicates panicle number, superscript refers to conidial number, the last two digits indicate year of collection; isolates followed by asterisks were used for partial resistance analysis of the cultivar BRS Colosso.

² Pathotypes identified using eight standard international differentials.

³ Pathotypes identified using eight Brazilian differentials.

⁴ Means disease severities followed by the capital letters in the line differ significantly, according to Tukey's test at the 0.05 probability.

⁵ Isolates followed by asterisks were utilized for determining partial resistance of rice cultivars BRS Colosso and BRS Bonança.

in aggressiveness (Table 2). For disease to occur the pathogen must be virulent; it may be virulent and strongly aggressive or weakly aggressive (Van der Plank 1975). The results in the present study showed, 10 of the 20 isolates were significantly more aggressive on BRS Colosso, independent of location and year of collection. Differences in aggressiveness of isolates pertaining to the same pathotype IB-1 were evident in inoculation tests on leaf. The damage level of rice cultivars could change over time not only due to change of race but also due to change in aggressiveness of the blast isolate belonging to the same race or lineage. A significant increase in aggressiveness of blast isolates in the cultivar C101A51 possessing *Pi-2* gene was observed. On the other hand aggressiveness of isolates from known durably resistant cultivars IR 64 and IR 36 was much lower than C101A51(Ahn 2000).

The analysis of variance of data on percentage leaf area affected and lesion size on culms, in inoculation test using 10 isolates of *M. oryzae* and two cultivars BRS Colosso and BRS Bonança are presented in Table 3. There was a highly significant main effect indicating difference in partial resistance between cultivars. There

Table 3 Analysis of variance for leaf blast severity¹ of rice cultivars BRS Colosso and BRS Bonança inoculated with 10 isolates of *Magnaporthe oryzae*

| Source | df | Sum of squares | Mean square | F value |
|--------------|----|----------------|-------------|---------|
| Cultivar (C) | 1 | 8398.40 | 8398.40 | 113.24* |
| Isolate (I) | 9 | 188.73 | 20.97 | 0.28 ns |
| CxI | 9 | 171.21 | 19.023 | 0.26 ns |
| Error | 20 | 1483.34 | 74.167 | |
| Total | 39 | 10241.70 | | |

¹ Disease severity data were transformed to $\arcsin \sqrt{x}$ for analysis; *F value significant at 0.1% probability levels.

was no significant difference in aggressiveness among isolates, with nine degrees of freedom, as well as cultivar x isolate interaction (Table 3). These results are in accord with those obtained by Yeh and Bonman (1986) and Araújo and Prabhu (2002). The main effects and the first order interaction determine aggressiveness of the isolates/partial resistance and virulence/vertical resistance, respectively. The inoculation tests with *M. oryzae* showed no evidence for vertical resistance in the cultivars BRS Colosso and BRS Bonança, because all 10 isolates were virulent considering percentage leaf area affected. The mean percentage leaf area of BRS Colosso (50.03%) was significantly higher than that of BRS Bonança (8.59%), indicating absence of adequate degree of partial resistance to leaf blast. The exotic source of resistance such as Key Bonnet, utilized as one of the parents in the cross, possibly with no partial resistance, might have contributed to the high vulnerability of BRS Colosso to blast.

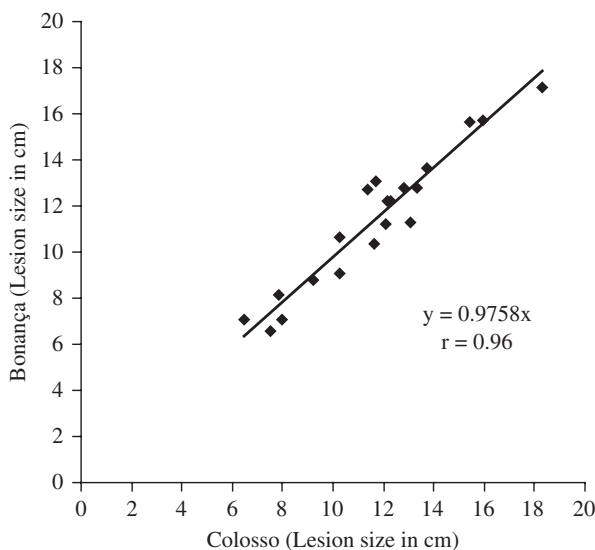
The analysis of data on culm blast showed significant isolate x cultivar interaction. Differences in lesion size on culm were significant (Table 4). A majority of the isolates on BRS Colosso were more aggressive than on BRS Bonança. Despite

Table 4 Leaf and culm blast severities inoculated with 10 isolates of *Magnaporthe oryzae* in greenhouse

| Isolate | BRS Colosso | | BRS Bonança | |
|-----------------------------|-----------------------|---------------------|--------------------|---------|
| | LBS(%) ¹ | CBS ² | LBS (%) | CBS |
| Py 9057-P1 ¹ -06 | 59.82 ^{ns} | 0.69 a ³ | 6.82 ^{ns} | 0.31 b |
| Py 8790-P2 ¹ -05 | 52.65 | 0.76 a | 15.74 | 0.52 ab |
| Py 9056-P4 ¹ -06 | 52.56 | 0.31 b | 8.69 | 0.37 ab |
| Py 8806-P3 ¹ -05 | 52.20 | 0.40 a | 10.56 | 0.21 b |
| Py 9061-P2 ¹ -06 | 49.90 | 0.57 a | 3.60 | 0.77 a |
| Py 8766-P2 ¹ -05 | 49.26 | 0.56 a | 4.58 | 0.15 b |
| Py 9063-P4 ¹ -06 | 48.12 | 0.54 a | 13.91 | 0.21 b |
| Py 8800-P2 ¹ -05 | 47.16 | 0.39 a | 6.22 | 0.51 ab |
| Py 9052-P1 ¹ -06 | 46.72 | 0.47 a | 6.44 | 0.30 b |
| Py 9053-P2 ¹ -06 | 41.95 | 0.50 a | 9.30 | 0.42 ab |
| Mean severity | 50.035 A ⁴ | 0.52 | 8.590 B | 0.38 |

¹ Leaf blast severity; ² Culm blast severity (disease index), ³ Letters followed by the same letter in the column do not differ significantly, according to Tukey's test (5%) ns = non-significant. ⁴ Means disease severities followed by the capital letters in the line differ significantly, according to Tukey's test at the 0.05 probability.

Fig. 1 Aggressiveness of field isolates of *Magnaporthe oryzae* on culms of cultivar BRS Colosso and BRS Bonança in inoculation tests using 19 isolates collected from affected panicles of BRS Colosso



differences in aggressiveness among isolates on these two cultivars, there was good correlation between lesion size of BRS Colosso and BRS Bonança in artificial inoculation test (Fig. 1). The interaction was of small magnitude. Significant interactions for partial resistance to leaf blast were reported in earlier studies (Bonman et al. 1989; Araújo and Prabhu 2002).

Occurrence of rice blast on widely grown susceptible cultivar such as BRS Bonança rarely attain damage levels similar to those of the cultivar BRS Colosso and is largely determined by agricultural practices such as late plantings and late application of N fertilizer as top dressing.

Leaf blast was not reported to occur in serious proportions on BRS Colosso both in early and late plantings. Leaf blast epidemics are characterized by a rapid increase of a disease to a distinct peak followed by decline, as the plant become more resistant with age. However, conidia from the infected leaves serve as inoculum for panicle infection. The increase in conidial production is exponential until the panicle emergence, independent of blast disease severity on leaves. The lack of inoculum or differences in quantity of inoculum is not a factor to be considered. The pathogen has sufficient time to multiply on leaves, abundant quantities of inoculum required for the panicle infection. Epidemics are likely to break out when a susceptible crop of BRS Colosso is exposed to abundant viable inoculum of a virulent pathogen originating from seed, under environmental conditions favorable for panicle infection. The role of infected rice seed as primary source of inoculum for initiating leaf blast epidemics in irrigated rice has been well documented (Lee 1994)

When both cultivars BRS Colosso and BRS Bonança are susceptible to the same pathotypes of the pathogen as is evident in the present study, a disease outbreak in one cultivar is expected to give rise to secondary outbreak in the cultivar planted at a later date. The infected plants of the earlier sown cultivar provide massive quantities

of inoculum for the later sown cultivar and is likely to be more severely attacked. But, blast disease outbreak similar to that observed on BRS Colosso have not been reported on BRS Bonança in farmers' fields, even in late plantings. In experimental fields of Embrapa Rice and Bean Research Center, when both BRS Bonança and BRS Colosso were planted in adjoining plots, the disease was destructive only on BRS Colosso but not on BRS Bonança which can be attributed differences in the degree of partial resistance to blast, in addition to the seed borne inoculum of the pre-existing pathotypes.

References

- Ahn, S. W. (2000). Spatial and temporal stability of genetic resistance to rice blast. In: Tharreau, D., Lebrun, M. H., Talbot, N. J., Notteghem, J. L. (eds.) *Advances in rice blast research*. Kluwer Academic Publishers, Dodrecht, pp. 162–171
- Araújo, L. G., & Prabhu, A. S. (2002). Somaclones da cultivar de arroz aromático Basmati-370 resistentes à brusone. *Pesq Agrop Bras* 37, 1127–1135
- Araújo, L. G., Prabhu, A. S., & Silva, G. B. (2005). Virulence pattern of *Pyricularia grisea* isolates from farmers' fields on newly released upland rice cultivars. *Fitopatol Bras* 30, 623–628
- Atkins, J. C., Robert, A. L., Adair, C. R., Goto, K., Kozaka, T., Yanagida, R., Yamada, M., & Matsumoto, S. (1967). An international set of rice varieties for differentiating races of *Pyricularia oryzae*. *Phytopathology* 57, 297–301
- Bonman, J. M., Bandong, J. M., Lee, Y. H., Lee, E. J., & Valent, B. (1989). Race specific partial resistance to blast in temperate Japonica rice cultivars. *Plant Dis.* 73, 496–499
- Correa-Victoria, F. J., & Zeigler, R. S. (1993). Pathogenic variability in *Pyricularia oryzae* at a rice blast "hot spot" breeding site in Eastern Colombia. *Plant Dis.* 77, 1029–1035
- Couch, B. C., & Kohn, L. M. (2002). A multilocus gene genealogy concordant with host preference indicates segregation of a new species, *Magnaporthe oryzae* from *M. grisea*. *Mycologia* 94, 683–693
- Kiyosawa, S. (1982). Genetics and epidemiological modeling of breakdown of plant disease resistance. *Annu Rev Phytopatol* 20, 93–117
- Kiyosawa, S., & Shiyomi, M. (1976). Simulation of the process of breakdown of disease resistant varieties. *Japan J Breed* 26, 339–352
- Lee, F. N. (1994). Rice breeding programs, blast epidemics and blast management in the United States. In: Zeigler, R. S., Leong, S. A., Teng, P. S. (eds.) *Rice blast disease*. CAB International, Wallingford, pp. 489–500
- Ling, K. C., & Ou, S. H. (1969). Standardization of the international race numbers of *Pyricularia oryzae*. *Phytopathology* 59, 339–342
- Notteghem, J. L. (1981). Cooperative experiment on horizontal resistance to rice blast. In: *Blast and upland rice – report and recommendations from the meeting for international collaboration in upland rice improvement*. International Rice Research Institute, Los Baños, pp. 43–51
- Ou, S. H. (1985). *Rice diseases*, 2nd edition, Commonwealth Mycology Institute, Kew
- Prabhu, A. S., Filippi, M. C., & Araújo, L. G. (2002a). Pathotype diversity of *Pyricularia grisea* from improved upland rice cultivars in experimental plots. *Fitopatol Bras* 27, 468–473
- Prabhu, A. S., Filippi, M. C., Araújo, L. G., & Faria, J. C. (2002b). Genetic and phenotypic characterization of isolates of *Pyricularia grisea* from the rice cultivars Epagri 108 and 109 in the State of Tocantins. *Fitopatol Bras* 27, 566–573
- Prabhu, A. S., Castro, E. M., Araújo, L. G., & Berni, R. F. (2003). Resistance spectra of six elite breeding lines of upland rice to *Pyricularia grisea*. *Pesq Agrop Bras* 38, 203–210

- Tarr, S. A. J. (1972). The principles of plant pathology. Winchester Press, New York
- Valent, B., & Chumley, F. G. (1994). A virulence genes and mechanisms of genetic instability in the rice blast fungus. In: Zeigler, R. S., Leong, S. A., Teng, P. S. (eds.) Rice blast disease. CAB International, Wallingford, pp. 111–134
- Van der Plank, J. E. (1975). Principles of plant infection. Academic Press, New York
- Yeh, W. H., & Bonman, J. E. (1986). Assessment of partial resistance to *Pyricularia oryzae* in six rice cultivars. *Plant Pathol* 35, 319–323