

## Durable resistance to rice blast disease – environmental influences

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*Key words:* environmental influence, *Oryza sativa*, *Pyricularia grisea*, *P. oryzae*, rice, rice blast

### Summary

Blast is one of the most serious diseases of rice worldwide. The pathogen, *Pyricularia grisea*, can infect nearly all parts of the shoot and is commonly found on the leaf blade and the panicle neck node. Host resistance is the most desirable means of managing blast, especially in developing countries. Rice cultivars with durable blast resistance have been recognized in several production systems. The durable resistance of these cultivars is associated with polygenic partial resistance that shows no evidence of race specificity. This partial resistance is expressed as fewer and smaller lesions on the leaf blade but latent period does not appear to be an important component. Partial resistance to leaf blast is positively correlated with partial resistance to panicle blast, although some cultivars have been found showing leaf-blast susceptibility and panicle-blast resistance. A diverse set of environmental factors can influence the expression of partial resistance, including temperature, duration of leaf-wetness, nitrogen fertilization, soil type, and water deficit. Because of the great diversity of rice-growing environments, resistance that proves durable in one system may or may not prove useful in another. In highly blast-conducive environments, other means of disease management must be applied to assist host-plant resistance.

### Introduction

Blast, a primary disease of rice worldwide, is caused by the fungus *Pyricularia grisea* (= *P. oryzae*) (Rossman et al., 1990). *P. grisea* is one of most widely distributed pathogens of rice, being found in nearly all rice-growing environments. The teleomorph of the pathogen, *Magnaporthe grisea*, has not been found in nature but can be produced in culture and is now used in several laboratories in studies of the genetics of the host-pathogen interaction (Valent, 1990). Blast disease remains a serious production problem in temperate and sub-tropical rice production areas, at high elevation in the tropics, and in tropical upland rice.

Aside from causing direct losses, the disease is also a constraint to increased production in many

marginal rice-growing environments because it is affected by crop management, particularly the use of nitrogen (N) fertilizer. In many parts of Asia where farmers practice intensive, high-input agriculture, blast frequently causes direct yield losses or increases production costs when fungicides are used for control. However, the disease is rarely found in areas where low-input, traditional rice culture is practiced because the farmers apply little or no N fertilizer. In many tropical upland areas where traditional rice cultivars are grown, farmers' fields show no disease. In yield trials, however, the same cultivars may show severe infection, even at relatively low fertilizer input levels. In such environments, the disease is a constraint to increased yields rather than a current production problem.

The epidemiological potential of blast is not only

associated with methods of crop management but is also linked to the rice production environment. There are five broad categories of rice environments: irrigated, rainfed lowland, upland, deep-water, and tidal wetland rice (Khush, 1984). These environments differ in their general conduciveness to blast. The disease has its greatest potential for causing severe epidemics in irrigated rice in temperate regions and in areas where rice is grown as an upland crop. It is not considered a major production problem in deepwater and tidal wetland rice.

Tropical lowland rice grown with good water control is the least prone to blast damage. In the Philippines and other parts of tropical Asia, the importance of the disease in lowland areas seems to have declined during the past 25 years. This decline was probably caused in part by the increase in the area of irrigated ricelands. Drought stress greatly increases the susceptibility of rice to blast; however, irrigation has lessened the probability of such stress. The change from traditional to modern cultivars may also be involved since indications are that some of the modern cultivars are more blast resistant than the traditional cultivars used in the past.

In spite of these improvements, the disease continues to be a problem in irrigated areas of tropical and sub-tropical countries, especially where blast-susceptible cultivars have been released (Loganathan & Ramaswamy, 1984). In fact, the disease re-emerged during the 1980s as an important production problem in both irrigated and rainfed regions of India (Reddy & Bonman, 1987), presumably because of the popularity of certain susceptible cultivars.

Developing resistant cultivars is the most desirable means of managing blast, particularly since small farmers can easily adopt technology packaged in the form of an improved cultivar. The importance of disease resistance in rice cultivars is often unrecognized. In some areas, blast disease is 'not a problem' because resistant cultivars grown prevent losses that would otherwise occur if susceptible cultivars were used.

### Resistance types and durability

Durable resistance to blast has been recognized in certain rice cultivars in certain environments (Bonman & Mackill, 1988; Johnson & Bonman, 1990). This durable resistance is associated with some specific characteristics of the resistance, again depending on the environment in question. In this discussion, three aspects of the type of resistance to leaf blast will be considered: its effects on pathogen reproduction, its inheritance, and its race specificity (Fry, 1982). Resistance to the neck blast phase of the disease will also be examined.

*Effects on pathogen reproduction: complete or partial.* Complete resistance to blast occurs when the fungus is unable to cause sporulating lesions on the plant. Complete blast resistance has been associated with spectacular 'breakdowns' in cultivar resistance. In Korea, the complete resistance of the Tongil cultivars was effective for 5 years before fungus races able to overcome that resistance appeared in 1976 (Lee et al., 1976). The weather during 1977 in Korea did not favour the disease and little blast was observed in the rice crop. In 1978, though, weather conditions favoured blast and by that time the pathogen had become established throughout the country; a devastating blast epidemic resulted (Crill et al., 1981). In Japan, the lifetime of complete resistance (termed 'true resistance' by Japanese researchers) appears to be about 3 years (Kiyosawa, 1982). Reiho, released in 1969 in Japan as a blast-resistant cultivar, possessed the gene *Pi-ta*<sup>2</sup> for complete resistance to Japanese races of *P. grisea*. Its area of cultivation increased until 1973, when it was severely damaged by blast (Matsumoto, 1974). Similarly, Reiho was completely resistant to races of *P. grisea* common in Egypt at its release in 1984. Resistance was lost during its first year in production, resulting in a serious epidemic (Reddy & Bonman, 1987). In Colombia, resistant cultivars have been released, but their resistance lasted only 1 or 2 years before being overcome by previously unidentified virulent races (Ahn & Mukelar, 1986). There do not seem to be any examples of complete blast resistance that have proved durable.

When a cultivar allows the pathogen to reproduce, yet not as much as a fully susceptible cultivar does, that cultivar has a form of resistance variously referred to as quantitative (Ahn & Ou, 1982), slow blasting (Villareal et al., 1981b), dilatory (Marchetti, 1983), field (Ezuka, 1979), or partial (Yeh & Bonman, 1986). The term partial resistance is used here for 'a form of incomplete resistance in which spore production is reduced even though the host plants are susceptible to infection (susceptible infection type)' (Parlevliet, 1979). A more recent definition of the term, 'quantitative resistance based on minor genes' (Parlevliet, 1988), is not adopted here because the genetic basis of blast resistance in most rice cultivars is unknown. Several examples of partial blast resistance are associated with durable resistance; one will be described in detail here.

In the Philippines and many other countries in Asia, the partially resistant cultivar IR36 has been cultivated in vast areas, but has rarely suffered damage due to blast. Its performance contrasts with that of IR50, which has often been blasted in wet season plantings (Loganathan & Ramaswamy, 1984). The complete resistance of IR36 and IR50 to some races appears to be identical because races that can infect IR36 can also infect IR50 and vice versa (Bonman et al., 1986). However, the two differ in level of partial resistance. When both are inoculated with compatible isolates, IR36 shows fewer and smaller lesions than does IR50 (Table 1). The difference is also evident in blast nursery mini-

plot tests (Yeh & Bonman, 1986). The latent period has been reported to be an important component of partial resistance to blast (Villareal et al., 1981a; Castano et al., 1989). However, IR36 and IR50 do not differ in latent period (Table 1). Similarly, no differences in latent period were found when a range of germplasm was tested at the International Rice Research Institute (IRRI) (E. Roumen, personal communication). Thus, infection efficiency and lesion size are the main components of the partial resistance that has been durable under tropical lowland conditions.

Partial resistance has also been described in many of the blast-resistant upland cultivars developed in West Africa and Brazil (Prabhu & Morais, 1986). At least one of these cultivars, Moroberekan, has shown durable resistance in the highly blast-conducive upland environments of West Africa (Bonman & Mackill, 1988). In most tropical upland areas, however, no cultivars with durable blast resistance have been identified. In Japan, traditional upland rice cultivars have a high level of partial resistance; the same cultivars have shown long-lasting resistance in upland culture, where blast is generally more severe (Toriyama, 1975). Although durable under Japanese conditions, the resistance of these cultivars was not sufficient against races present in Latin America (K. Toriyama, personal communication). Thus, the level of partial resistance that proves durable in one environment may not necessarily be useful in other, more blast-conducive environments.

Table 1. Components of partial resistance in two rice cultivars: susceptible IR50 and durably resistant IR36

Resistance component	Cultivar	
	IR36	IR50
Lesions per dm <sup>2</sup> fully extended fifth leaf	3	31
Lesions per dm <sup>2</sup> partially extended sixth leaf	31	345
Lesion size (mm <sup>2</sup> )	1.6	4.0
Latent period (days)	5.7	5.7

Adapted from Yeh & Bonman (1986).

*Inheritance.* Much of the work on inheritance of complete blast resistance has been done in Japan, where 13 major genes have been identified (Ezuka, 1979). Major resistance genes are common in rice germplasm, and even the most susceptible cultivars will show complete resistance to some isolates of the fungus. Few systematic studies have been conducted using tropical rices, but recent work at IRRI in the Philippines indicates that one or two dominant genes present in the cultivars studied confer complete resistance against each fungus isolate (Yu et al., 1987). Several of the genes identified at IRRI have been incorporated into a common susceptible background through backcrossing, their allelic re-

relationships determined (Mackill & Bonman, 1992), and their chromosomal location mapped using molecular markers (Yu et al., 1991). The relationship between the major genes identified in Japan and at IRRI is now under investigation.

Partial resistance is generally inherited through an undetermined number of minor genes, as is the case with tropical lowland (Wang et al., 1989) and upland rice (Notteghem, 1985). However, there is at least one exception to this generalization – the single gene *Pi-f* controls partial resistance in Japanese cultivars St 1 and Chugoku 31 (Toriyama, 1975).

Recently, restriction fragment length polymorphism (RFLP) mapping has been applied to the study of partial resistance in rice (Wang, 1992). The durably resistant rice cultivar Moroberekan was crossed with a highly susceptible cultivar CO39. Recombinant inbred (RI) lines were produced by single seed descent and analyzed with 100 RFLP markers. Field and greenhouse tests indicated the presence of partial resistance in the RI lines. To characterize this resistance, a single isolate was used in polycyclic tests, and each line was scored for lesion number, lesion size, and diseased leaf area. Fourteen RFLP markers defining 10 chromosomal segments were associated with effects on lesion number. The six markers with the strongest effects accounted for 62% of the variance for lesion number. Most of the loci identified affected all three of the parameters measured. Thus, partial resistance in the traditional rice cultivar Moroberekan is of complex inheritance. Future work will determine the practical utility of marker-based selection for improving blast resistance in rice.

*Race specificity.* From the previous discussion, it is clear that complete resistance is race-specific in that a cultivar may show resistance to some races of the pathogen but may be infected by other races. Such specificity has also been found in partially resistant cultivars with the *Pi-f* gene. St 1 and Chugoku 31 were partially resistant to races of *P. grisea* in Japan at the time of their release, but their resistance later broke down because new races evolved (Toriyama, 1975). Race-specific partial resistance was also encountered when susceptible

Korean japonica cultivars tested at IRRI showed partial resistance (Bonman et al., 1989). Inoculation experiments revealed that these cultivars' resistance to Philippine races was race-specific. The cultivars showed few sporulating lesions with Philippine isolates but many such lesions with Korean isolates (Fig. 1). Resistance against the Philippine isolates was not due to lower aggressiveness in the pathogen, since the susceptible control cultivar CO 39 was equally susceptible to both sets of isolates. It is likely that this race-specific partial resistance is simply inherited.

It is not known if polygenic partial resistance can be race-specific. Using different partially resistant lowland cultivars, Yeh & Bonman (1986) found no evidence of isolate-cultivar interaction. Villareal et al. (1981b) reported 'the occurrence of differential interaction' between rice cultivars and isolates of the pathogen for components of partial resistance. At least one of the cultivars they studied, IRAT 13, has polygenic partial resistance (Notteghem, 1985). Similarly, pathologists in Brazil empirically observed that resistance in IRAT 13 had 'eroded' after having been sown for several years at the same highly blast-conducive site (A. Prabhu, personal communication). This field observation should be substantiated with tests using isolates collected over several years.

*Neck blast resistance.* Most research on blast resistance has focused on leaf blast, which occurs at the vegetative stage of crop development. During this phase of the disease, the fungus infects the leaf blades and leaf collars thus reducing the photosynthetic capability of the plant directly by reducing leaf area and indirectly via physiological effects (Baastians, 1991). However, the pathogen can also infect the panicle after flowering. When the panicle neck node, branches, and spikelets are attacked and colonized, the flow of photosynthates to the developing grains is reduced or completely inhibited. Infection of the panicle neck node, called 'neck blast', is the most destructive stage of the disease because it causes direct yield loss (Bonman et al., 1991). For convenience, screening for blast resistance is often done at the early vegetative stage, with the assumption that lines found resist-

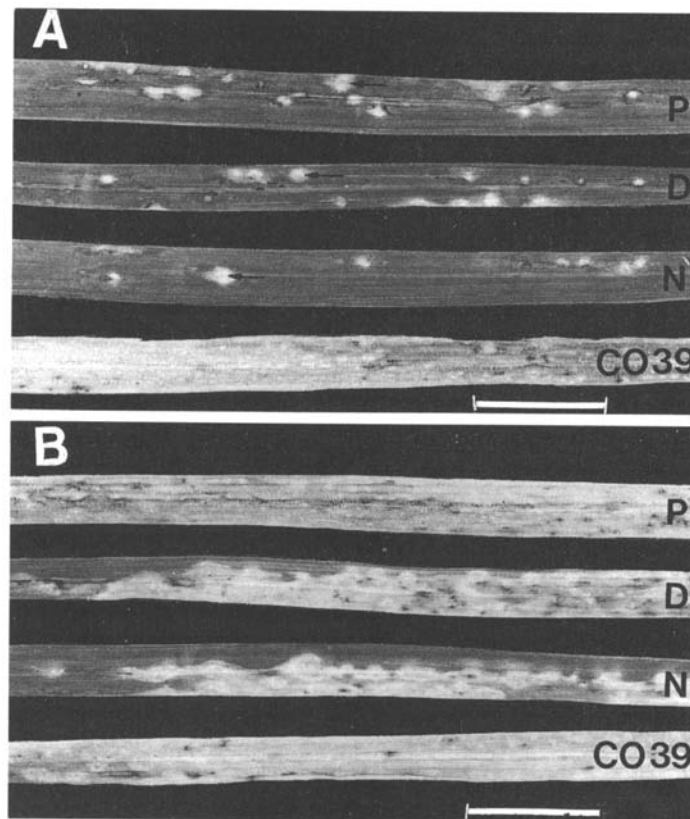


Fig 1. Reactions of Korean japonica rice cultivars Palgeum (P), Daechang (D), and Nagdong (N) and susceptible control CO39 inoculated with isolates of *Pyricularia grisea* from (A) the Philippines and (B) Korea. Arrows indicate typical individual lesions caused by the Philippine isolate. Scales bar = 1 cm (Adapted from Bonman et al., 1989a).

ant to leaf blast will also be resistant to neck blast (Ou, 1985). Similarly, resistance studies are also more convenient using leaves rather than panicles.

There is evidence that leaf and neck blast resistance are linked. In early work, cultivars completely resistant to a particular race at the seedling stage were also completely resistant to neck infection and those susceptible at the seedling stage were likewise susceptible to neck infection (Ou & Nuque, 1963). Researchers sometimes report a lack of correspondence between tests of leaf blast and neck blast resistance. Part of this discrepancy may be due to environmental differences at the different times various test cultivars flower. However, there is increasing evidence that relative differences in resistance exist among cultivars, especially when detailed measurements of partial resist-

ance are made (Chung et al., 1980; Hwang et al., 1987; Bonman et al., 1989b).

The level of neck blast resistance was measured in 27 lowland rice lines in three field plantings at IRRI (Bonman et al., 1989b). The results for neck blast were compared with the leaf blast resistance of the same lines measured in several nursery experiments. The two sets of data showed positive correlation ( $r^2 = 0.66$ ) (Fig. 2). The correlation was highest when the means of the three plantings were used. This may indicate errors due to differences in maturity of the entries in any single planting. Some lines appeared to be exceptions to this general relationship. For example, IR25604 was more susceptible to leaf blast but more resistant to neck blast than the partially resistant control IR36. Thus, although resistance to leaf and to neck blast

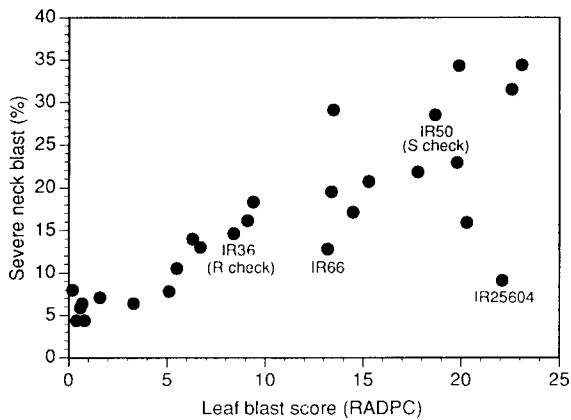


Fig. 2. Relationship between resistance to neck blast and resistance to leaf blast in 27 rice lines. Neck blast measurements are from five lowland field plantings and leaf blast measurements are from four upland miniplot trials. RADPC = the relative area under the disease progress curve. (Adapted from Bonman et al. 1989b).

are usually positively correlated, some cultivars may be relatively resistant to one phase of the disease and relatively susceptible to another.

Neck blast is the most economically important phase of the disease. In some rice-growing areas, damage from leaf blast is a production problem, but as a general rule neck blast is responsible for most of the yield loss due to blast. The amount of loss in grain yield measured in field trials in the Philippines and Korea was positively correlated with the percentage of panicles with severe neck blast infection (Fig. 3). The Philippine trials also demonstrated the value of neck blast resistance in preventing yield losses. In the experiments cultivar IR66 was one of the test entries. This cultivar is susceptible to leaf blast but resistant to neck blast (Fig. 2) (Bonman et al., 1989a). Although its leaf blast infection was equal to that of the susceptible control IR50, IR66 had a low incidence of neck blast and no yield loss relative to plots protected with fungicide. Thus, neck blast resistance alone was sufficient to protect the crop from loss due to blast (Bonman et al., 1991).

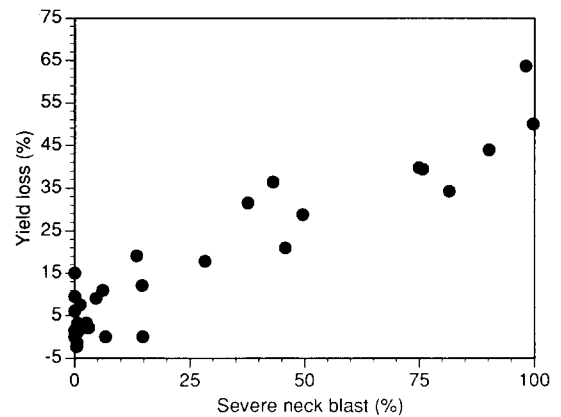


Fig. 3. Relationship between yield loss and percentage severe neck blast as measured in field trials in Korea and the Philippines. (Adapted from Bonman et al., 1991).

### Environment and durability of resistance

Blast disease is greatly affected by the environment. The key environmental factors favouring disease are 1) night temperatures between 17 and 23°C, 2) long duration of leaf wetness, 3) N fertilization, 4) aerobic soil, 5) water deficit, and 6) still air at night. Environmental influence is primarily through the effects on the physiology of the host, on the pathogen itself, or on the host-pathogen interaction.

The effect of aerobic soil is probably a direct effect on host susceptibility. Recently, Osuna-Canizalez et al. (1991) showed that plants given  $\text{NO}_3^-$ -N in nutrient solution culture were much more susceptible than plants given  $\text{NH}_4^+$ -N. They concluded that N form may be the mechanism causing plants grown in aerobic soil to have higher susceptibility to blast, since  $\text{NO}_3^-$ -N is the predominant N form under aerobic conditions.

Long duration of leaf wetness has a direct effect on the pathogen. At optimum temperature (about 25°C), the pathogen can infect the host after 6–8 hours of wetness. At about 16°C, though, infection occurs later (16–20 hours).

Temperature affects the interaction between the host and the pathogen. High temperatures (above 28°C) favour the growth of *P. grisea* but also stimulate host resistance. Plants are more susceptible at lower temperatures (about 20°C), thus favouring

infection even though pathogen growth at these temperatures is slower.

As well as the six factors described, the soil type also affects the susceptibility of rice to blast disease. In the Philippines, for example, field observations indicated that upland rice grown at the Santo Tomas testing site in Batangas Province generally showed much less blast than rice grown at the Cavinti testing site in Laguna Province. E. Kurschner et al. (unpublished results) found that the site differences could be attributed to differences in the soil at the two sites. For two seasons at each site, plants were grown in pots containing soil from Cavinti and in pots containing soil from Santo Tomas. Disease was always highest in the Cavinti soil (Table 2).

Because of the many strong, complex, and interacting effects of environment on blast, there is great diversity in the 'disease potential' of various sites. Disease potential is a measure of the conduciveness of the environment to the disease and is affected by climatic, edaphic, and hydrologic conditions as well as the agronomic practices of farmers. There is at present no quantitative measure of blast disease potential for rice-growing environments, but blast simulation models may eventually prove useful in predicting the potential for the disease in regions where rice production practices are changing.

For blast disease, the durability of resistance not only is a function of the genotype of the host, but

also is dependent upon the disease potential of the environment. In less blast-conducive environments, such as most tropical lowland areas, a level of partial resistance to leaf and neck blast similar to that of IR36 will probably be sufficient provided it is of the durable type. It may even be possible for the partial resistance to neck blast of cultivars like IR66 to show durability despite leaf blast susceptibility.

In environments with higher disease potential, such as temperate irrigated rice and probably some tropical rainfed lowland areas, a higher level of partial resistance will be required. For each target environment, field experiments using cultivars with various degrees of partial resistance should be conducted to ascertain the resistance level useful for blast management. Empirical studies are at present the only way of obtaining this information, since blast simulation models are not yet sophisticated enough to account for the many interacting plant and environment variables that affect the amount of disease that occurs. Once the required level of partial resistance is known, appropriate controls can be chosen for use in segregating populations generated by breeding programmes.

In environments with very high blast potential, such as many upland sites, it may not be possible to obtain high yields and at the same time manage blast disease solely with partial resistance. It is unlikely, for example, that the level of partial resistance in a cultivar such as IR36 would be of any direct use in most tropical upland environments. At the same time, it is important to recognize the value of such resistance in the appropriate target environment. For areas with very high blast potential, it will probably be necessary to incorporate major gene resistance into genotypes with high levels of partial resistance and to develop and use crop management practices that minimize disease development.

Certain cultivars show durable resistance because they '... remain resistant ... even though they are extensively cultivated in environments favourable to disease' (Johnson, 1981). Johnson's concept of durable resistance has been useful for scientists involved in rice improvement because it focuses on a practical issue: the utility and long-

Table 2. Effect of soil on leaf blast on potted plants grown at two upland rice testing sites for two years

	Site			
	Santo Tomas soil		Cavinti soil	
	Santo Tomas	Cavinti	Santo Tomas	Cavinti
1988	0.03 c	1.94 a	0.03 c	0.43 b
1989	0.65 b	2.26 a	0.28 c	0.56 b
Means	0.34 bc	2.10 a	0.15 c	0.50 b

Data are percentage leaf areas diseased 45 days after seeding; mean of two rice cultivars.

Means within a row followed by a common letter are not significantly different by LSD ( $p = 0.05$ ).

Unpublished data from E. Kurschner, J.M. Bonman, I. Müller, J. Breithaupt & J. Kranz.

evity of resistance in farmers' fields. The application of the concept in rice research has led to a much clearer understanding of how blast can be managed using resistant germplasm in the remarkably diverse environments in which the crop is produced.

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