Resistance

Stability of Partial and Complete Resistance in Rice to *Pyricularia grisea* Under Rainfed Upland Conditions in Eastern Colombia

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ABSTRACT

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Two sets of experiments were conducted to compare the relative stability of partial and complete resistance in rice to *Pyricularia grisea* (causal agent of the rice blast disease) in a disease "hot spot" in eastern Colombia. In the first set of experiments, 186 breeding lines selected at the site over the F_2 to F_4 generations, ranging from completely to partially resistant in the F_4, were evaluated under heavy disease pressure at the site every season from 1987 to 1990 (two seasons per year). A set of 92 lines from the International Rice Blast Nursery (IRBN) with initial evaluations of "resistant" (standard evaluation system [SES] ≤ 5), also ranging from completely to partially resistant, were evaluated under the same conditions. Locally developed materials were rated as susceptible less frequently than lines from the IRBN set. In both sets, significantly fewer lines initially scored as highly resistant (SES = 1 to 3) were later scored as susceptible (SES > 5) or showed any increase in susceptibility to local pathogen populations compared to those initially rated as partially resistant (SES = 4 to 5). In the second set of experiments, locally developed and exotic lines were grouped according to partial (few susceptible-type lesions [SES type 5]) and high resistance (few resistant-type lesions [SES type 1 to 3]). After three seasons of evaluation, lines with high levels of resistance had a significantly lower rate of change to susceptible levels. The rice cultivar Oryzica Llanos 5 was selected at this site from a line with complete blast resistance and was released for commercial cultivation in blast-prone eastern Colombia. It is grown on approximately 5×10^4 ha/year and has remained resistant to blast over 10 consecutive growing seasons, both in experimental blast nurseries and in farmers' fields where blast normally is a severe problem. This cultivar also showed uniformly high levels of blast resistance when evaluated at seven high blast level sites in four Asian countries in blast nurseries with 72 other cultivars with differing levels and origins of blast resistance. The results suggest that selecting high levels of resistance when diverse sources are combined can be used to develop cultivars with stable resistance to rice blast.

Additional keywords: *Magnaporthe grisea, Oryza sativa, Pyricularia oryzae*.

Rice blast, caused by *Pyricularia grisea* Sacc. (teleomorph *Magnaporthe grisea* (Hebert) Barr.) is a major constraint to rice (*Oryza sativa* L.) production, particularly under the rainfed conditions prevalent in Latin America. Since many rice growers in developing countries do not have access to fungicides, cultivar resistance has been the preferred means of controlling the disease. Developing durably resistant rice lines, therefore, is a high priority for most rice-breeding programs where rice blast may occur.

High levels of resistance to the blast pathogen are, however, of notoriously short duration (11,16). Many cultivars with resistance conferred by a few major genes have quickly shown susceptible reactions after release. The great pathogenic diversity of the pathogen populations combined with the presumed relative ease of overcoming resistance conferred by a single major gene may explain the lack of durability (3).

Cultivars may exhibit compatible lesion types but also have low disease levels. These cultivars exhibit fewer and smaller blast lesions than fully susceptible cultivars, and spore production may be reduced (1). Such "partial resistance" (27) has been durable in some temperate cereals (13). Definitions of partial resistance have changed from one based on phenotype: "a form of incomplete resistance in which spore production is reduced even though the host plants are susceptible to infection (susceptible type)" (27), to one based on genotype: "quantitative resistance based on minor genes" (26). Most breeders selecting for partial resistance use the first definition because it is virtually impossible to know the genetic composition of segregating, or even advanced, breeding materials (1,2). Selection for partial resistance to *P. grisea*, therefore, is based on the development of relatively fewer or smaller compatible lesions compared to highly susceptible cultivars (2,31). In this paper, we will use this operational understanding of partial resistance.

Selecting for partial resistance to rice blast is difficult because of the pathogen's low heritability (29) and its complexity (25,27). The most recent strategy advanced for selecting for partial resistance to *P. grisea* involves making meticulous greenhouse inoculations with highly compatible isolates on segregating progeny (F_2 to F_4) and discarding the most susceptible plants (28). Very few, if any, rice-breeding programs have the resources to evaluate blast resistance in this manner. Rice-breeding programs typically have many simultaneous objectives. At the International Rice Research Institute (IRRI), Manila, the Philippines, for example, 50,000 entries in the pedigree nursery alone may be evaluated for blast resistance every year. Consequently, breeding for partial resistance usually involves simply selecting plants showing intermediate disease levels over several generations, discarding both

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highly susceptible and highly resistant plants (2). Breeding lines usually are grown in a blast nursery or in fields conducive to blast disease development.

It has been suggested that in environments not conducive to the development of severe epidemics, such as tropical and temperate irrigated lowlands, partial resistance may offer adequate protection from the blast pathogen (1,2,21,31). However, blast epidemics have occurred on cultivars with partial resistance in Korea (7,8,9) and in the southern United States, where partial resistance of local cultivars is thought to be responsible for the relative unimportance of rice blast (20). The use of partial or horizontal resistance also has been proposed for managing blast in upland environments (23,24).

In 1985 the Rice Program at the International Center for Tropical Agriculture (CIAT), Cali, Colombia, initiated blast-resistance breeding at a site (Santa Rosa) in eastern Colombia known for high pathogen diversity and reliable disease pressure (4,6). The population was composed of at least six pathogen lineages (18), determined by DNA fingerprinting using the repetitive probe MGR586 (10,19). We reasoned that the continuous challenge by a diverse pathogen population should reduce the risk of breakdown of a putatively resistant breeding line due to escape and allow for early warning if new pathotypes emerge. Furthermore, if genotypes with partial resistance were selected and evaluated under continuous blast pressure, their relative usefulness and durability could be compared to genotypes with high levels of resistance.

The purpose of this research was to investigate the stability of resistance to rice blast in genotypes developed using this approach and to compare stability in those genotypes with high levels of resistance with those possessing partial resistance (relatively few compatible lesions). We tested the hypothesis that more durable host resistance could be obtained by selecting for intermediate (presumably partial) resistance than by selecting for high levels of resistance. In one set of experiments, a set of 186 F_5 breeding lines with varying levels of resistance and 92 entries from the International Rice Blast Nursery (IRBN) were evaluated for changes in leaf area affected. In a second set of experiments, 151 locally developed and exotic lines were evaluated for changes in lesion type on the leaf and neck. Genotypes were evaluated in a highly blast-conducive environment for eight growing seasons in 4 years. The rice cultivar Oryzica Llanos 5 (OL5) developed from this breeding program, released in 1989 for a highly blast-conducive environment, was evaluated under blast-conducive conditions in eight sites in five countries to evaluate its resistance over a range of environments.

MATERIALS AND METHODS

Rice blast nursery management. The CIAT rice blast-resistance breeding station, Santa Rosa, is located approximately 20 km east of Villavicencio, Colombia (310-m elevation, 4° N latitude and 73° W longitude, on alluvial soils, pH 4.0 to 5.0, and 3.0 to 4.0% organic matter), in an important rice-growing area where rice blast is one of the principal production constraints. The growing season extends from April to January with mean maximum and minimum temperatures of 30 and 21°C, respectively, and 2,500-mm of rainfall on average. Uniform distribution of rain makes two consecutive rice crops possible: April through September (season A) and October through January (season B).

High blast levels were maintained in breeding plots by planting spreader rows under conditions conducive to blast development (high seeding density [3.0 g/m] and high nitrogen level [150 to 200 kg of N per ha]) prior to sowing breeding populations. Spreader rows were composed of cultivars susceptible to all local pathotypes (5) and included: i) commercial cultivars that were released as resistant in the region but that were currently susceptible to subsets of the pathogen population under production conditions (Cica 4 [10%]; Cica 8 [10%], Cica 9 [10%], Metica 1 [10%], and Oryzica 1 [10%]); ii) the resistant source Ceysvoni, used in the breeding program and known to be susceptible to some pathotypes of the blast fungus (10%); and iii) cultivar Fanny, highly susceptible to most local pathotypes (40%). Abundant, naturally occurring inoculum was supplemented with chopped infected leaves that were harvested from pure plots of all spreader components, air-dried, mixed, and added to the spreader rows early in the season. Three check cultivars (Cica 8, Oryzica 1, and Ceysvoni) sharing different spectra of susceptibility (5,18) were planted every 20 rows to monitor uniformity of disease severity. A set of 45 rice cultivars with different resistance genes was planted monthly at different sites of the station to monitor shifts in the pathogen population.

The disease-enhancement approach performed satisfactorily during the course of this study. Plants in spreader rows always were highly diseased, and the susceptible check cultivars always exhibited susceptible reactions in the field. Variations in weather, such as a prolonged dry period, could reduce disease severity, but there was no evidence of major fluctuations in the composition of the inoculum over the study period. However, cultivar Ceysvoni, which was highly resistant at the outset of the study, began to exhibit some susceptible-type lesions after several growing seasons, indicating that some virulence shift was occurring in the pathogen population

Selection and evaluation. After the spreader rows had substantial blast levels (usually about 2 weeks after emergence), breeding lines were planted in 5-m rows oriented perpendicular to the spreader rows and parallel to the prevailing wind direction. Rice blast severity in breeding lines was evaluated twice during the leaf stage at approximately 30 and 45 days after seeding (tillering to booting growth stages), whereas neck blast incidence was evaluated once at the late dough stage (25 days after heading) using the standard evaluation system (SES) for rice (12). Leaf blast: 0 = no visible lesions; 1 = small brown pin-point size or larger brown specks with no signs of sporulation; 2 = small roundish to slightly elongated, necrotic gray spots, 1 to 2 mm in diameter, mostly restricted to lower leaves with no sporulation; 3 = small roundish to slightly elongated, necrotic gray spots, 1 to 2 mm in diameter, abundant on upper leaves; 4 = narrow or slightly elliptical (spindle shaped) lesions, 3 mm or longer, showing sporulation under high relative humidity (lesions "typical" for susceptible reaction), covering less than 2% of leaf area; 5 = typical blast lesions covering 2 to 10 % of leaf area; 6, 7, 8, and 9 = typical compatible blast lesions covering 11 to 25, 26 to 50, 51 to 75, and >75% of leaf area, respectively. Lines with consistent reactions of 4 and 5 were considered to have partial resistance to leaf blast (1). SES for panicle blast was based on the percentage of plants with blast lesions completely around the last internode, the neck, or the lower part of the panicle axis with 0 = no incidence; 1 = <5%; 3 = 5 to 10%; 5 = 11 to 25%; 7 = 26 to 50%; and 9 = >50%. There are no ratings of 2, 4, 6, and 8.

Stability of resistance of selected breeding lines and IRBN entries. The breeding lines included in these experiments previously had been evaluated in the F_2 to F_4 generations at Santa Rosa, and generation advance followed the pedigree method. The IRBN (received from the International Rice Testing Program at IRRI) is a set of diverse lines nominated from breeding programs around the world and with demonstrated blast resistance in at least one site for several seasons. The IRBN is a genetically diverse set of lines. The nursery for 1986 was planted at Santa Rosa, Colombia, under conditions similar to those used for the breeding lines. Lines showing various levels of symptom development during the first year were selected from the IRBN for subsequent studies on the stability of their resistance.

Breeding lines (186) from 50 crosses were selected and evaluated as resistant in the F_2 to F_4 generations and used to monitor the stability of resistance identified under Santa Rosa selection conditions. Selected lines had resistance levels of very high (SES

= 1 to 3) to partial (SES = 4 and 5). All selected lines exhibited neck blast reactions of ≤5. Entries (92) from the 1986 IRBN were used to compare the blast resistance of exotic and locally selected genotypes. Beginning in 1987 (season A), all lines were planted in the Santa Rosa breeding fields in two 5-m rows per plot (two replications of plots) with 150 kg of N per ha applied in equal fractions at 20, 40, and 65 days after planting; 30 and 60 kg of P and K per ha, respectively, at sowing. Weeds were controlled with herbicides depending on the species present. Plantings were made during seasons A and B from 1987 through 1990. Seed for the experiment was harvested in bulk from the 1987 (season A) test plots. Breeding lines evaluated were, therefore, F_5 in the first season and were unselected bulk populations from each previous generation in subsequent generations.

Stability of resistance selected according to lesion type. Lines of exotic and locally generated materials (151) distinct from the breeding and IRBN lines were selected according to their leaf and neck lesion types (SES) at Santa Rosa. Lines were preevaluated (under nursery conditions similar to those described above) for lesion type, diseased leaf area, and neck blast reaction. Lines included in this study had different combinations of symptom severity. Only lines from crosses evaluated and selected in Santa Rosa were considered "local"; all others were "introduced." SES leaf lesion types were: 0 to 3, as described above; 5 = narrow or slightly elliptical lesions, 1 to 2 mm in diameter, more than 3 mm long, with a brown margin; 7 = broad spindle-shaped lesions with yellow, brown, or purple margins; and 9 = rapidly coalescing whitish, grayish, or bluish lesions without distinct margins. SES for neck lesion types were: 0 = no visible lesions or lesions on only a few pedicels; 1 = lesions on several pedicels or secondary branches; 3 = lesions on a few primary branches or the middle part of the panicle axis; 5 = lesions partially around the panicle base (node), the uppermost internode, or the lower part of the panicle axis near the base; 7 = lesion completely around the panicle base, the uppermost internode, or the panicle axis near the base with more than 30% of filled grain; and 9 = lesion completely around the panicle base, the uppermost internode, or the panicle axis near the base with less than 30% of filled grains. There were no ratings of 2, 4, 6, and 8 for leaf and neck lesion types. Lines included had leaf and neck lesion types (SES = 1 to 3) or susceptible lesion types (SES ≥ 5) in all combinations with highly resistant (SES < 5), intermediate (SES = 5), and susceptible (SES > 5) neck blast reactions. The lines were planted in season A of 1988, 1989, and 1990, under the conditions described above, and evaluated following the procedures described above.

TABLE 1. Changes in reaction of rice lines to *Pyricularia grisea* over eight seasons of evaluation

Rice line Line no.	Original rating[a]	No. of lines with final rating			
		1–3	4	5	>5
Breeding[b]					
86	1–3	39	16	21	10
58	4		13	15	30
42	5			11	31
IRBN[c]					
41	1–3	7	4	7	23
31	4		5	1	25
20	5			1	19

[a] Evaluation scale: resistant (1–3) = absence of lesions or nonsporulating, small lesions covering less than 1% of leaf area; moderately resistant (4 and 5) = typical blast lesions covering less than 2% or 2 to 10% of leaf area, respectively; and susceptible (>5) = susceptible-type lesion covering more than 10% of leaf area.

[b] Breeding lines developed at the Santa Rosa breeding and experimental station at the Centro Internacional de Agricultura Tropical, Meta, Colombia.

[c] IRBN = International Rice Blast Nursery, International Rice Research Institute, Manila, the Philippines.

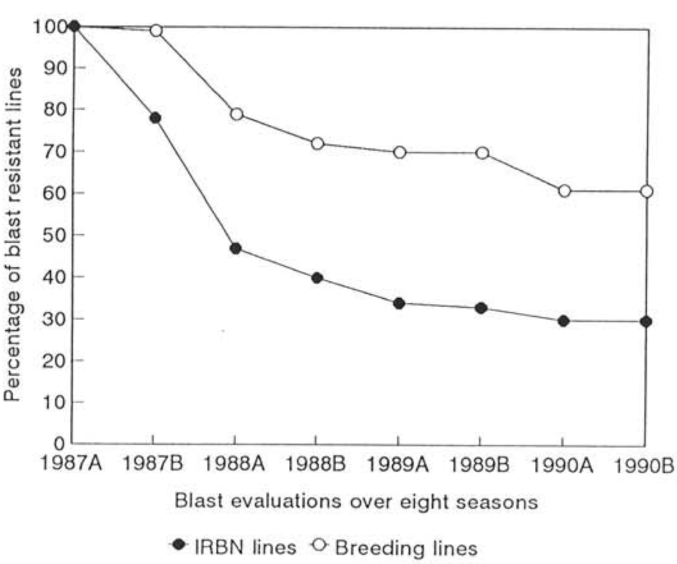

Fig. 1. Percentage of rice lines remaining resistant to *Pyricularia grisea* over eight seasons (two seasons per year, A and B) of field evaluations. Initial number of lines was: 92 advanced lines of the International Rice Blast Nursery (IRBN), International Rice Research Institute, Manila, the Philippines, and 186 F_4 breeding lines developed at a blast "hot spot" site in Colombia.

Evaluation of the stability of the resistance of a commercial cultivar. Cultivar OL5 was released for commercial rice production in Colombia in 1989 as blast resistant (17). OL5 also was evaluated in Santa Rosa and was included in a set of nurseries dispatched to collaborating rice scientists in Colombia, Indonesia, Korea, the Philippines, and Thailand. Nurseries were grown in highly blast-prone environments from 1992 to 1994 and managed in the same manner as the IRBN.

RESULTS

Stability of resistant breeding and IRBN lines. Although disease pressure was somewhat lower during season B, lines that were rated as fully susceptible (SES > 5) remained susceptible in subsequent seasons. Thus, cumulative numbers of susceptible lines from year to year are used in all comparisons.

Changes in the reaction of rice breeding and IRBN lines to *P. grisea* over eight seasons of evaluation differed according to their origins and their initial levels of resistance (Table 1). The number of lines rated as resistant for all variables in both the Santa Rosa breeding and IRBN lines declined over the eight seasons (Fig. 1).

TABLE 2. Number of rice lines from the IRBN and breeding line groups[a] showing any increase in susceptibility to *Pyricularia grisea* and showing change from resistant (rating 1–3) or moderately resistant (rating 4–5) to susceptible (rating >5) reactions over eight seasons at Santa Rosa, Meta, Colombia

Group	No. of lines			
	No increase in susceptibility[b]	Increased susceptibility	Remained at ≤5	Changed to >5
Breeding	63	123	115	71
IRBN	13	79	25	67
	$\chi^2 = 12.30$[c] $P < 0.001$		$\chi^2 = 29.56$ $P < 0.001$	

[a] Breeding lines developed at the Santa Rosa, breeding and experimental station at the Centro Internacional de Agricultura Tropical, Meta, Colombia; IRBN = International Rice Blast Nursery, International Rice Research Institute, Manila, the Philippines.

[b] Evaluation scale: resistant (1–3) = absence of lesions or nonsporulating, small lesions covering less than 1% of leaf area; moderately resistant (4 and 5) = typical blast lesions covering less than 2% or 2 to 10% of leaf area, respectively; and susceptible (>5) = susceptible-type lesion covering more than 10% of leaf area.

[c] Chi-square test (2 × 2 contingency tables) and level of significance.

Over the first three seasons, both groups showed a rapid decline in the percentage of lines rated as resistant to the pathogen population. The IRBN group showed a substantially greater rate of decline over this period. The total decline from the 1987 season A evaluations was approximately 73% for the IRBN group compared to only 38% for the breeding lines. After the 1988 B season, the remaining resistant lines in both groups showed more stability, with similar declines of approximately 10 and 8% of the IRBN and breeding lines, respectively, evaluated as field susceptible.

The frequency of lines initially classified with very high to intermediate resistance, which showed no change in susceptibility, was significantly different for the Santa Rosa and IRBN lines (Table 2). The frequency of IRBN lines that increased in susceptibility rating was greater than for the breeding lines. Likewise, the distribution of resistance category changes differed among the two (Table 2). The lines that changed from resistant to susceptible ratings differed significantly in their initial field reactions (Table 3). For each initial level of resistance, there was less increase in rating for the local breeding lines than for the introduced IRBN lines.

Similarly, breeding lines with high initial levels of resistance increased in susceptibility rating less frequently than those with intermediate initial resistance evaluations (Table 3). There were no differences among IRBN lines (Table 3). The rating of highly resistant breeding lines (1 to 3) increased in susceptibility less often than IRBN lines with the same evaluation.

The 68 breeding lines with ratings less than 5 after eight seasons of evaluation (Table 1) came from 27 crosses. For 11 of these crosses, no initially selected progeny was rated greater than 4 (21 lines). Of the 29 parents in these 11 crosses, only 3, IR46, Taichung176, and Tox95, were not also involved in crosses that yielded susceptible progeny (rated 5 and above). There were 6 crosses that had no progeny ever rated 4 or above, for a total of 15 lines. Cultivar C46-15 was the only common parent in each of the 6 crosses, although it was susceptible in Santa Rosa. All parents were susceptible to some isolates collected from Santa Rosa; however, not all sources of resistance could be included in the spreader rows.

Lesion type. Within the group of 151 exotic and locally generated materials, rice lines with neck blast resistance (SES < 5) and with highly resistant leaf lesion types (SES = 1 to 3 and less than 1% of leaf area affected) did not increase in susceptibility rating as frequently as lines with intermediate or susceptible reactions. This was observed when either total lines with susceptible leaf lesion types covering less than 10% of leaf area (113 lines) or lines with less than 2% of leaf area affected (105 lines) were compared (Table 4). The lines with resistant or intermediate reactions developed under Santa Rosa conditions increased in susceptibility rating significantly less often than lines with resistant or intermediate reactions that were introduced to Santa Rosa conditions (Table 5).

The remaining lines had resistant or susceptible lesion types but low leaf area affected and intermediate (SES = 5) or susceptible (SES > 5) neck blast reactions. As long as the neck blast reaction was intermediate or susceptible, disease rating tended to increase regardless of the initial lesion type and diseased leaf area rating (data not shown).

Resistance of OL5. OL5 was highly resistant at both leaf and panicle stages in all sites where the disease nurseries were planted (Table 6).

TABLE 3. Number of rice breeding and IRBN lines[a] showing changes in susceptibility to *Pyricularia grisea* as a function of initial reaction after eight seasons in Santa Rosa, Meta, Colombia

	No. of breeding lines (%)				No. of IRBN lines (%)			
Initial evaluation[b]	Remained at ≤5	Changed to >5	Stable evaluation	Increased susceptibility	Remained at ≤5	Changed to >5	Stable evaluation	Increased susceptibility
1–3	76 (41)	10 (5)	39 (21)	47 (25)	18 (20)	23 (25)	7 (8)	34 (37)
4	28 (15)	30 (16)	13 (7)	45 (24)	6 (7)	25 (26)	5 (5)	26 (28)
5	11 (6)	31 (17)	11 (6)	31 (17)	1 (1)	19 (21)	1 (1)	19 (21)
	$\chi^2 = 50.3$[c] $P < 0.0001$		$\chi^2 = 7.87$ $0.05 < P < 0.01$		$\chi^2 = 11.7$ $0.001 < P < 0.01$		$\chi^2 = 1.76$ n.s.[d]	

[a] Breeding lines developed at the Santa Rosa, breeding and experimental station at the Centro Internacional de Agricultura Tropical, Meta, Colombia; IRBN = International Rice Blast Nursery, International Rice Research Institute, Manila, the Philippines.

[b] Evaluation scale: resistant (1–3) = lesion types 1, 2, or 3 (resistant types) and less than 1% of leaf area affected; moderately resistant (4) = lesion type 5 (susceptible type) with less than 2% of leaf area affected; moderately resistant (5) = lesion type 5 with 2 to 10% of leaf area affected; and susceptible (>5) = susceptible-type lesion covering more than 10% of leaf area.

[c] Chi-square test (3 × 2 contingency tables) and level of significance.

[d] n.s. = not significant.

TABLE 4. Number of rice lines with resistant- or susceptible-type lesions caused by *Pyricularia grisea* but low leaf area affected, showing no increase or an increase in susceptibility after 3 years in Santa Rosa, Meta, Colombia

Initial lesion type[a]	Leaf area affected (%)	Leaf and neck reaction after 3 years: Unchanged	Increased
1–3	<1	37	23
5	<10	21	32
		$\chi^2 = 5.47$[b] $0.01 < P < 0.05$	
1–3	<1	37	23
5	<2	17	28
		$\chi^2 = 5.78$ $0.01 < P < 0.05$	

[a] Evaluation scale: resistant (1–3) = lesion types 1, 2, or 3 (resistant types) and less than 1% of leaf area affected; moderately resistant (5) = lesion type 5 with 2 to 10% of leaf area affected.

[b] Chi-square test (2 × 2 contingency tables) and level of significance.

TABLE 5. Number of rice lines evaluated as highly and moderately resistant to *Pyricularia grisea*, with unchanged or increased susceptibility after 3 seasons in Santa Rosa, Meta, Colombia, as a function of their origins

Origin[a]	No. of lines[b]: No increase in susceptibility	Increased susceptibility
Santa Rosa	39	22
Introduced	16	28
	$\chi^2 = 8.43$[c] $P < 0.01$	

[a] Santa Rosa = advanced lines developed under Santa Rosa conditions since early generations; introduced = advanced lines developed at locations other than Santa Rosa.

[b] Includes those lines evaluated as having lesion types 1–3 and less than 1% of leaf area affected and lines lesion type 5 and less than 2% of leaf area affected.

[c] Chi-square test (2 × 2 contingency table) and level of significance.

DISCUSSION

Breeding lines with the lowest initial disease level in the field were the most durably resistant, and those originating from the local breeding population were more durably resistant than introduced resistant lines. Relatively stable blast resistance was obtained in this study by selecting "partially" resistant lines showing moderate symptom development. However, stable blast resistance occurred more frequently among lines with high initial levels of resistance than among those with intermediate levels of resistance. This difference was observed whether any increase in susceptibility was considered or if only changes from resistant to highly susceptible were considered. Our results demonstrate that high levels of resistance are stable in some lines. Therefore, selection strategies for durable resistance that discard highly resistant lines (2,24) should be reconsidered.

Materials developed at Santa Rosa did not shift from resistant to susceptible ratings as frequently as the introduced lines. Introduced lines with high levels of initial resistance were not any more stable than those with intermediate resistance. A genotype must be subjected to several seasons of evaluation in the presence of a representative pathogen population to accurately judge its value; therefore, high levels of resistance selected from rice populations with diverse combinations of resistance genes in the presence of a diverse and abundant pathogen population may yield lines with stable blast resistance. Achieving the required inoculum diversity and abundance demands meticulous management of a nursery located in an environment reliably conducive to rice blast disease development.

The objective of conducting a breeding program in a rice blast disease "hot spot" is to increase the chances of developing lines that have stable resistance to the pathogen relative to other methods. The results of this study suggest that this objective is being met: 62% of the local breeding lines continued to show high levels of blast resistance to the local pathogen population after 10 seasons in this high disease environment, whereas all Colombian commercial cultivars developed using a variety of other methods were susceptible at or shortly after release. The selection and test period apparently was sufficient for even low-frequency compatible pathotypes to attack previously resistant lines. However, three generation (F_2 to F_4) of selection were not sufficient to identify lines with resistance. There was a fairly rapid erosion of resistance over the first four cycles after selection followed by relative stability.

Crosses among "field-susceptible" cultivars may yield progeny showing high levels of resistance to the same pathogen population. The local breeding lines in this study originated from crosses from a blast resistance gene-pyramiding project (30), and compatible races have been identified in Santa Rosa for all resistance sources used (5). Thus, specific gene combinations may explain the stability of certain lines, suggesting that pyramiding nonallelic major genes may be used to develop durable resistance to blast (3,15).

TABLE 6. Performance of rice cultivar Oryzica Llanos 5 (OL5) under severe rice blast disease conditions in nurseries in five countries

Site	No. of seasons	No. of cultivars[a]	% cultivars susceptible[b]	Reaction of OL5[b]
Cavinti, Philippines	2	69, 72	77.8	0
Los Banos, Philippines	2	73,73	64.5	0
Kon Kaen, Thailand	2	69, 71	56.5	0
Phrae, Thailand	1	59	33.9	1
Ubon, Thailand	2	71, 54	40.7	0
Suweon, Korea	1	73	39.5	0
Sitiung, Indonesia	3	71, 73, 73	72.6	0
Santa Rosa, Colombia	1	73	91.8	2

[a] Number of cultivars that germinated and survived for blast disease susceptibility evaluation. Multiple values indicate number of cultivars tested in each year.

[b] Evaluated following the 0–9 Standard Evaluation System for Rice (12). A susceptible reaction is indicated by a rating of 4 or more, consisting of increasing diseased leaf area of expanding sporulating lesions. 0 = immune, 1 = pin-prick necrotic lesion, 2 = nonsporulating brown necrotic lesion, 3 mm or less in diameter.

The high levels of resistance to blast reported here are probably due to major genes (5). Rice breeders and pathologists are explicitly discarding major genes when they discard plants with high levels of resistance, believing that this resistance will eventually break down. We propose that potentially useful resistance genes are being discarded. With careful nursery management in a blast-conducive environment, these genes promise to be powerful tools in disease management. However, under less stringent selection conditions, use of these genes may not provide adequate resistance longevity.

The nature of partial resistance suggests that it should be effective in areas where the disease pressure is usually low (1). However, in many rice-growing areas blast-conducive conditions do occur during some years. Planting cultivars with levels of partial resistance that may be insufficient under certain environmental conditions places farmers in a difficult situation regarding chemical control, because fungicides must be applied at the first signs of disease. Farmers may apply fungicides and risk an economic loss from a possibly unnecessary application, or they may wait for further disease development and risk a major production loss. Use of partial resistance for blast sometimes may compromise one objective of disease-resistance breeding: reduced risk and chemical applications. Developing high levels of multigenic resistance for disease-prone environments is an attractive, and apparently achievable, alternative to partial resistance. Recently, major blast-resistance genes have been discarded in favor of selection for quantitative resistance. The growing number of mapped minor and major resistance genes and development of marker-aided selection suggests that quantitative blast-resistance genes may be efficiently combined with the major genes (22,32).

OL5 was released from the CIAT program in 1989 (17) as a modern, high-yielding, blast-resistant cultivar for the very blast-prone eastern plains of Colombia. It is widely grown in this region (5×10^4 ha/year) and remains highly resistant after 10 seasons of cultivation. Blast resistance of commercial cultivars in this region has been very short lived. The modern cultivar with the, heretofore, most durable blast resistance, Oryzica 1, was highly susceptible to local pathogen populations early in its third season of cultivation (R. S. Zeigler, *personal observation*).

OL5 has shown a remarkable durability in resistance over space as well as over time. It had a virtually unmatched degree of resistance when evaluated in several highly blast-conducive sites in Asia (Table 6). OL5 also was inoculated with 172 isolates from 13 Colombian genetic lineages at CIAT (4) and with 202 isolates from 6 genetic lineages from the Philippines at IRRI (32). To date, no compatible isolates have been found for this cultivar. The resistance most probably is multigenic, because all its ancestors were susceptible to isolates from Santa Rosa (F. J. Correa-Victoria and R. S. Zeigler, *unpublished data*). The effectiveness of the resistance in OL5 over very different locations suggests that analysis of the resistance of this cultivar may provide insights into the nature and genetics of its durable resistance.

We do not assume that OL5 will remain resistant indefinitely, and this is not problematic if a dynamic breeding program is in place. Indeed, cultivar replacement is desirable for improvement of a range of agronomic traits. Oryzica Llanos 4, produced from the same program but from a different cross and released the same year, began to show susceptibility to the field population of *P. grisea* at Santa Rosa after nine seasons and could eventually experience high levels of disease in the field.

The approach described here has yielded extremely high and, heretofore, unobtainable levels of blast resistance. Following Johnson's (14) definition of durability (cultivation for many seasons over large areas under disease-conducive conditions) and considering that the cultivar has withstood challenges from very different and widely dispersed populations, OL5 can be considered a durably blast-resistant cultivar. This resistance has been achieved in a high-yielding background. If the concepts that explain the development of this resistance hold true (33), rice blast disease may be effectively managed through high levels of durable resistance.

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