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S. Veillet · M. C. Filippi · A. Gallais

Combined genetic analysis of partial blast resistance in an upland rice population and recurrent selection for line and hybrid values

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Abstract The CNA-IRAT 5 upland rice population has been improved for 4 years by recurrent selection for blast resistance in Brazil. In order to predict the efficiency of recurrent selection in different test systems and to compare the relative advantage of hybrids versus pure line breeding, a combined genetic analysis of partial blast resistance in the CNA-IRAT 5 population was undertaken. A three-level hierarchical design in inbreeding and a factorial design were derived from the base population. Partial blast resistance of lines and hybrids was evaluated in the greenhouse and in the field by inoculation with one virulent blast isolate. The means and genetic variances of the hybrids and lines were estimated. Genetic advance by recurrent selection was predicted from estimates of variance components. The inheritance of partial blast resistance was mainly additive but non-additive effects were detected at both levels of means and variances. Mean heterosis ranged from 4%–8% for lesion size and lesion density to 10–12% for leaf and panicle resistance. High dominance or homozygous dominance variances relative to additive variance and negative covariance between additive and homozygous dominance effects were estimated. A low frequency of favourable alleles for partial resistance would explain the observed organisation of genetic variability in the base population. Recurrent selection will efficiently improve partial blast resistance of the CNA-IRAT 5 population. Genetic advance for line or hybrid values was expected to be higher testing doubled haploid lines than S1 lines, or than general combining ability. Two components of partial resistance assessed in the greenhouse, lesion size and lesion density, could be used as indirect selection criteria to improve field resistance. On the whole, hybrid breeding for partial blast resistance appeared to be slightly more advantageous than pure line breeding.

Key words Quantitative genetics · Recurrent selection · Partial resistance · *Magnaporthe grisea* · *Oryza sativa* L.

Introduction

Rice blast, caused by the fungus *Magnaporthe grisea* (Hebert), is the most devastating rice disease worldwide. In the tropics, the most economical way of controlling this disease is by growing resistant cultivars. Unfortunately, in most cases the resistance of these cultivars breaks down a few years after they are released: the major genes selected to confer a high level of blast resistance have been rapidly bypassed by virulent races. Breeding for durable resistance became an important challenge in the 1980s, especially with respect to upland cropping systems where blast disease is even more serious. Partial resistance would be more durable, as in most host-pathogen combinations, if it were quantitatively inherited and not race-specific (Bonman 1992). Very little is known about the genetic determinism of partial blast resistance, with partial resistance being defined here as the resistance expressed when compatible isolates are inoculated. A few authors have shown that partial resistance can usually be considered as any quantitative trait (Wang et al. 1989; Wang et al. 1994; Roumen 1993).

Blast pathogen attacks the leaves, at the vegetative stage, and the necks or the panicles, at the reproductive one. Genetic variability for blast resistance at both

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S. Veillet[1](✉)
Centro Nacional de Pesquisa Arroz-Feijão, CNPAF/EMBRAPA, 74000 Goiânia Goias, Brazil

M. C. Filippi
Centro Nacional de Pesquisa Arroz-Feijão, CNPAF/EMBRAPA, 74000 Goiânia Goias, Brazil

A. Gallais
Institut National Agronomique Paris-Grignon, 16 rue Claude Bernard, F-75232 Paris cedex 05, France

Present address:
[1] Station de Génétique Végétale, INRA-UPS, Ferme du Moulon, 91190 Gi. f sur Yvette, France

stages has already been observed, but the genetic relationship between panicle and leaf resistance is not clear. Positive correlations between both traits were reported in most cases with some exceptions (Bonman 1992). Field leaf resistance can be broken down into a few components of slow-blasting resistance such as lesion size or lesion density (Parlevliet 1979). These components are usually assessed in the greenhouse by inoculation with compatible blast isolates, and they could be used advantageously as selection criteria, providing they are correlated with field resistance. Field leaf resistance seems to be mainly determined by lesion size and lesion density, but the genetic nature of this relationship has never been investigated (Villareal et al. 1981; Roumen 1993).

Recurrent selection for partial resistance would be the most efficient breeding strategy by which to improve the blast resistance durability of rice cultivars (Notteghem 1993). Since 1989 an important recurrent selection programme to improve the CNA-IRAT 5 upland rice population for grain yield, grain shape, drought and blast resistance has been conducted at the Centro Nacional de Pesquisa Arroz-Feijão (CNPAF/EMBRAPA) in Brazil (Veillet 1993). Three recurrent selection schemes for partial blast resistance to the virulent blast isolate ECJ5P'88 were compared: mass selection in the greenhouse, mass selection in the field and S1 selection in the field. A genetic analysis of partial blast resistance in this wide-genetic base population would allow us to tentatively predict the efficiency of recurrent selection for partial blast resistance.

Both pure line and hybrid varieties can be derived from CNA-IRAT 5 at different steps of recurrent improvement. Although only pure lines have been released up to now in Brazil, hybrid breeding is an important part of the Brazilian rice improvement programme (Veillet 1993). In China, 50% of the rice area was cultivated with F_1 hybrids by the end of the 1980s, and these yielded 20–30% more than the traditional pure line cultivars. While high levels of heterosis for a self-pollinated species have been reported for most traits, very little is known on the relative blast resistance of hybrids versus pure lines (Virmani and Edwards 1983). Moreover, the prediction of blast resistance heterosis with parental values has never been discussed.

As stated by Gallais (1990), the relative importance of line or hybrid breeding from a segregating population theoretically depends not only on the amount of mean heterosis but also on the ratio between the line and hybrid genetic variances. A breakdown of the genetic variability of both kinds of varieties would help us to better understand the inheritance of partial resistance and, furthermore, predicted genetic gains following different selection methods could be compared. The description of genetic variability in multiallelic populations with different levels of inbreeding is very complex (Gillois 1964; Harris 1964; Cockerham 1983). In the absence of epistasis, five components of genetic variance are involved, and these have been only rarely estimated as heavy experimental designs have to be derived (Gallais 1977, 1984; Cornelius and Dudley 1976).

An original genetic design combining factorial and hierarchical design in inbreeding was derived from the CNA-IRAT 5 population, and partial blast resistance of the hybrids and lines was broken down into genetic components. The objectives of this genetic analysis of blast resistance were (1) to study the expression of heterosis for partial blast resistance; (2) to breakdown the genetic variance among lines and hybrids; (3) to compare the predicted efficiency of three recurrent selection procedures; and (4) to evaluate the efficiency of indirect selection on resistance components for field resistance improvement.

Materials and methods

Genetic designs

The upland rice population CNA-IRAT 5 was synthesised at CNPAF (Goiânia, Goiás, Brazil) in order that recurrent selection could be applied to rice breeding. Twenty-seven *japonica* upland rice cultivars from South America and West Africa and 1 *indica* irrigated cultivar from the Philippines were intercrossed (Taillebois and Guimarães 1989). The recessive *ms* gene for male sterility was introduced into the population from the male-sterile Asian cultivar 'IR36' in order to facilitate the recurrent recombinations (Singh and Ikehashi 1981)). After three random matings in the field and the subsequent harvesting of male-sterile plants, one hierarchical design in inbreeding and one factorial design in crossing were derived from the base population. The three-factor hierarchical design was first created deriving 154 *S*4 lines from 36 *S*0 plants keeping 3 *S*1 plants per *S*0 and 2 *S*2 plants per *S*1. More than 15 *S*2 families per *S*1 line were checked for male sterility at the flowering stage, and all of the segregating families were discarded in order to conserve only completely fertile lines. Further observations in *S*3 confirmed the success of the male-sterility gene elimination. Remnant seeds from 36 *S*2 families were conserved to obtain data on early generations. The factorial design was composed of three 6 × 6 independent factorials, crossing a subset of 36 lines derived from different *S*0 plants. Eighty-six F_1 hybrids were obtained with enough seeds for field experiments.

Greenhouse and field experiments

The 154 lines, 36 *S*2 families and 86 hybrids were evaluated for blast resistance at CNPAF in the greenhouse and in the field during the rainy season 1991/1992 in a randomised complete block design with two replications. One monoconidial blast isolate (ECJ5P'88) belonging to the international race IB-9 and compatible with 24 of the 28 parental cultivars of CNA-IRAT 5 was inoculated in both environments. The greenhouse experiment was planted and inoculated in two phases, corresponding to the two replications, during the year 1992. Rice plants were grown in plastic flats (23 × 33 × 12 cm) divided in ten rows of 10 plants. Each genotype was represented by one row per replication. Basal fertilizer was applied before planting in the proportions of 0.6-1.5-0.8 g of N-P-K per flat of 6 kg of soil, with an additional top dressing of 0.6 g of N per flat 20 days after planting. Rice plants were inoculated 27 days after sowing by spraying a spore solution of ECJ5P'88 adjusted to 2.5×10^5 spores per milliliter sterile distilled water onto the leaves, 30 ml per flat. Inoculated plants were placed for 24 h in dew chambers at 25 °–29 °C with a relative humidity higher than 90% and then transferred to a growth cabinet. Disease severity, i.e. lesion type, lesion density and lesion size, was recorded 7 days after inoculation on the last leaf of 10 plants per plot. Lesion type was recorded according to the scale proposed by Prabhu (1989b). Those genotypes with more than 60% of the plants having typical sporulating lesions were considered to be compatible to the blast isolate. Inheritance of complete resistance was investigated using the factorial and hierarchical designs in order to detect the main resistance genes. Lines and hybrids completely resistant or segregating were eliminated from the partial resistance analysis in the greenhouse and in the field. Lesion density and lesion size were evaluated using the visual scales described by Notteghem (1985). Plot means between the classes were calculated and log-transformed in order to normalise the distributions.

The field experiment was planted in December 1991 under upland conditions at the CNPAF experimental farm (Goiânia, Goiás, Brazil). Experimental plots consisted of one 2-m row sown at a density of 25 seeds per meter with 0.30 m between rows. Five spreader rows situated perpendicular to those of the testing plots were planted at a high density with 2 cultivars susceptible to ECJ5P'88. Basal fertilizer was applied before planting at the rate of 10-60-30 kg of N-P-K per hectare, and the rows were top-dressed 20 days after planting with 60 kg of N per hectare. The spreader band was inoculated 40 days after planting by spraying with a spore solution of ECJ5P'88 adjusted to 2.5×10^5 spores per milliliter of distilled water. Field leaf resistance was scored 20 days after inoculation by evaluating the percentage of infected area of two upper leaves per plant for 10 plants per plot according to the 0–12 visual scale proposed by Horsfall (1945). Field panicle resistance was rated 25 days after heading by assessing the percentage of sterility caused by blast of two panicles per plant for 10 plants per plot according to the 0–9 visual scale proposed by the IRRI (1976). The heading date was recorded when 50% of the rice plants per plot had eared. Plot means between the classes were calculated and log-transformed in order to normalise the distributions.

Statistical models

Multivariate analyses of variance were performed at the plot mean level for each generation in each environment using the statistical computer package SAS (SAS Institute 1988), which provides least-square estimates of parameters. Only the genotypes compatible to ECJ5P'88 were included in these analyses. All effects were declared to be random, except the block one, and genetic and residual (co) variances were estimated using Henderson's method III.

The hierarchical model for breaking down the value Y_{ijkl} of one line deriving from the *ith* S0 plant, the *jth* S1 plant and the *kth* S2 plant in the *lth* replicate is as follows:

$$Y_{ijkl} = \mu + S0_i + S1(S0)_{ij} + S2(S1{*}S0)_{ijk} + b_1 + R_{ijkl}$$

where $S0_i$ is the S0 effect with variance $\sigma^2_{gL(0)}$; $S1(S0)_{ij}$ is the S1 effect in the *ith* S0 plant with variance $\sigma^2_{gL(1)}$; $S2(S1{*}S0)_{ijk}$ is the S2 effect in the *jth* S1 plant in the *ith* S0 plant with $\sigma^2_{gL(1)}$; $S2(S1{*}S0)_{ijk}$ is the S2 effect in the *jth* S1 plant in the *ith* S0 plant with variance $\sigma^2_{gL(2)}$; b_1 is the fixed block effect; and R_{ijkl} is the residual with variance σ^2_{rL}. The S0 effect was tested on the $S1(S0)$ effect, which was itself tested on the $S2(S1{*}S0)$ effect. S2 families were analysed using the classical two-way analysis of variance. Genetic variance among S2 families (σ_{gS2}), residual variance (σ^2_{rS2}) and genetic covariance between S2 and S2-derived lines ($\sigma_{g(L,S2)}$) were estimated.

The factorial model for breaking down the value Y_{ijkl} of the hybrid between the *jth* female and the *kth* male in the *ith* factorial and the *lth* replicate is as follows:

$$Y_{ijkl} = \mu + G_i + F_{ij} + M_{ik} + FM_{ijk} + b_1 + R_{ijkl}$$

where G_i is the factorial effect with variance σ^2_{gG}; F_{ij} is the female effect in the *ith* factorial with variance σ^2_{gF}; M_{ik} is the male effect in the *ith* factorial with variance σ^2_{gM}; FM_{ijk} is the interaction between male and female effect in the *ith* factorial with variance σ^2_{gFM}; b_1 is the fixed block effect; and R_{ijkl} is the residual error with variance σ^2_{rH}. Male and female effects were tested on the male-female interaction effect. The genetic correlation between the line value of the hybrid parents and their general combining ability, $\sigma^2_{g(L,gca)}$, was calculated.

Prediction of heterosis

The partial resistance of the hybrids and lines were compared with Student's test. Mean heterosis was estimated by considering the S4 lines to be completely homozygous and was expressed in percentage of the line value. S2 family means were not reported because of the low number of completely compatible bulks leading to imprecise mean estimates. Mean line values and general combining abilities of the parental lines were compared for their efficiency to predict hybrid value and heterosis by linear regression and tested for significance with the *F*-test. The relationship between heterosis and genetic divergence was investigated using Mahalanobis distance between parental lines as predictor. Mahalanobis distance was calculated on the basis of 12 agro-morphological traits recorded on the 36 parental lines in one field experiment in 1991/1992. Of the variation observed, 71% was explained by 5 traits: grain length, plant height, number of days to heading, leaf length and leaf width.

Breakdown of genetic variance

Without epistasis, the genetic covariance between inbred relatives is a function of five variance components. Gallais (1974) gave the general expression of the covariance between two inbred relatives *X* and *Y*:

$$\mathrm{Cov}(X,Y) = 2\phi_{(i/i)}\mathrm{var}\,A + \phi_{(ij/ij)}\mathrm{var}\,D + 4\phi_{(i/ii)}\mathrm{cov}\,AD_o + \phi_{(ii/ii)}\mathrm{var}\,D_o + (\phi_{ii/ii)} + \phi_{(ii/jj)} - F_x F_y)\sum D_o^2$$

where var A and var D are the additive and dominance variance; var AD_o is the covariance between the additive and homozygous dominance effects; var D_o is the homozygous dominance variance; $\sum D_o^2$ is the sum over loci of the squared inbreeding effects; F_x and F_y are the inbreeding coefficients of *X* and *Y*; $\phi_{(ij/kl)}$ is the generalised coefficient of kinship between *X* and *Y* with *i*, *j*, *k*, l representing the identity classes of the genes in both genotypes.

The genetic variance among homozygous lines, var*L*, or between hybrids, var *H*, can be easily derived from this general expression:

$$\mathrm{Var}\,L = 2\mathrm{var}\,A + \mathrm{cov}\,AD_o + \mathrm{var}\,D_o = \sigma^2_{gL(0)} + \sigma^2_{gL(1)} + \sigma^2_{gL(2)}$$

$$\mathrm{Var}\,H = \mathrm{var}\,A + \mathrm{var}\,D = \sigma^2_{gF} + \sigma^2_{gM} + \sigma^2_{gMF}$$

The description of the genetic variance among lines and hybrids is then a function of only four components. As we considered the S4 lines to be homozygous, $\sum D_o^2$ was not estimated. Nine genetic (co) variances were available from the statistical design, which can be expressed as a function of the variance components (Appendix 1). Least-square estimates of variance components were computed for the complete one-locus model, and another one was restricted to additivity and dominance; both models were compared and tested for goodness-of-fit. Standard errors of the variance components were estimated assuming balanced designs. Combined residual variances were estimated by least-square at the plot level from the residual variance of the three generations.

Prediction of genetic advance

Expected genetic advance for the varietal value, ΔG_v, from one cycle of recurrent selection is, according to a general expression given by Gallais (1990),

$$\Delta G_v = i\theta \frac{\mathrm{cov}(TV)}{\sqrt{\mathrm{var}\,T}}$$

where *T* is the value of the genotypes according to the test system; *V* the varietal value of the genotype after intercrossing; *i* the selection intensity; $\theta = 1$ or 2 according to the control of selection on one or two sexes. A general expression of heritability, h_v^2, in recurrent selection comes from this formula (Gallais 1990):

$$h_v^2 = \frac{2\mathrm{cov}(TV)}{\mathrm{var}T}$$

Broad-sense heritabilities and genetic advance for direct selection between lines and hybrids from the base population were calculated stating that $2\mathrm{cov}(TV)$ and var T were respectively the overall genetic or residual design variance among lines or hybrids. The selection rate used for genetic advance prediction was 1%. Predicted heterosis between the 1% best hybrids and lines was estimated from the predicted means of selected hybrids and lines.

Narrow-sense heritabilities and genetic advances in recurrent selection were estimated in the restricted model for the three test systems that could be easily derived within 2 years: *S*1 families, di-haploid lines (DH lines) and general combining ability (GCA). DH lines could be derived from the base population by anther culture, and the general combing ability could be assessed by crossing male-sterile plants from *S*1 families with a tester. Theoretical expectations of the phenotypic variance in the test system and of the covariances between the test value and the line or hybrid values were calculated using the general expression of the covariance between two genotypes (Appendix 2). We assumed that the experimental designs were similar in the three test systems with the families replicated twice, and that both the residual variance and the selection intensity ($i = 1.65$) were the same. Note that one recurrent selection cycle would take three to four generations whatever generation test is used, that is to say 2 years in tropical countries with two cropping seasons per year.

Indirect selection on resistance components

Genetic correlations between field resistance and components of partial resistance for pure line and hybrids were calculated. Indirect genetic advance for leaf and panicle field resistance was predicted using the design (co)variances between lines and hybrids and compared to direct univariate genetic advance for four combinations of resistance traits as predictors. We compared the efficiency of both indirect selection in the greenhouse for field resistance and indirect selection on leaf resistance for panicle resistance to direct univariate selection. We discussed the use of lesion size and lesion density as associated traits in the prediction of field resistance. A selection index was constructed for leaf and panicle resistance with economical weights chosen as the inverse genetic standard deviations of each trait in order to provide comparable genetic advance for both traits.

Results

Prediction of heterosis

A total of 107 lines (including 27 hybrid parents), 16 *S*2 families and 49 hybrids were compatible to the inoculated isolate and were evaluated for partial resistance. In the population studied complete resistance to ECJ5P'88 blast isolate was mainly controlled by one single dominant gene present at a high frequency ($P = 0.3$). Most lines and hybrids completely resistant in the greenhouse were not diseased in the field.

Heterosis ranged from 4–8% of the line value when assessed in the greenhouse to 10–12% when estimated in the field (Table 1). In the field, the hybrids had a smaller area of diseased leaf and a lower panicle sterility caused by blast. In the greenhouse, fewer and smaller blast lesions succeeded in developing on the hybrids.

General combining ability was a significant predictor of heterosis, with coefficients of correlation ranging from 0.3 to 0.6 (Table 2). Line value was negatively correlated with heterosis as had been theoretically expected. General combining ability and to some degree line value were significantly correlated to hybrid value (Fig. 1). In fact, line value was highly correlated to general combining ability for all resistance components. Combining ability and line value should be used jointly to detect the best hybrid combinations from parental values. The efficiency of Mahalanobis distance as a predictor of heterosis is null.

Table 1 Line mean, hybrid mean and heterosis for partial blast resistance assessed in the field and in the greenhouse

Traits	Line mean	SD[a]	Hybrid mean	SD	Heterosis (%)
Field leaf resistance	2.531	0.038	2.224	0.073	12***
Field panicle resistance	3.769	0.073	3.405	0.123	10***
Greenhouse lesion density	2.687	0.042	2.572	0.092	4*
Greenhouse lesion size	3.648	0.059	3.360	0.082	8***

*,*** Level of significance of the difference between hybrid and line means tested with Student's test, 5% and 0.1%, respectively

[a] Standard deviation for a confidence interval at $P = 0.95$

Table 2 Prediction of heterosis with line value, general combining ability and Mahalanobis distance

Traits	Coefficient of correlation with heterosis		
	Line value	GCA	D^2 [a]
Field leaf resistance	– 0.20	0.58***	0.02
Field panicle resistance	– 0.15	0.58***	0.12
Greenhouse lesion density	– 0.30*	0.45**	0.25
Greenhouse lesion size	– 0.44**	0.42**	0.01

*,**,*** Level of significance of the linear regression to predict heterosis, 0.1%, 1%, 5%, respectively

[a] D^2: Mahalanobis distance

Breakdown of genetic variance

Genetic and residual design (co)variances estimates are reported in Appendix 3. Most genetic design effects were significant at 5% when tested on the residual. However, the estimates of some components of variance were negative, such as the male-female interaction variance for field resistance and some effects were no more significant when tested on the nested effect. No significant reciprocal effect was detected, which means that only nuclear genes were involved in partial resistance expression.

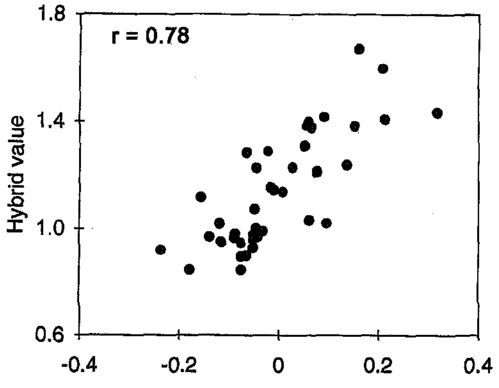

Fig. 1 Representation of the correlation between hybrid value and general combining ability for field leaf resistance to blast

The genetic variance among hybrids was more than twice that among lines for leaf resistance and lesion density (Table 3). Phenotypic variance was significantly higher between hybrids than between lines, whereas residual variance among hybrids was significantly smaller for both traits. Phenotypic or residual variances were not significantly different between hybrids and lines for panicle resistance and lesion size. Yet genetic variance of lesion size was smaller between hybrids than between lines.

The restricted model fitted well with the genetic design (co)variances, explaining at least 44% of the observed variation (Table 4). Additive variance was significantly different from zero for all traits in inbreeding or in crossing as tested by analysis of variance (Appendix 3), representing from 50% to 100% of the single-cross genetic variance. Dominance variance was significantly different from zero for lesion size, lesion density but slightly negative for leaf and panicle resistance assessed in the field. In fact, the strictly additive model would fit as well the genetic variation of partial resistance in the field. The use of one combined residual variance for genetic advance prediction was justified by the goodness-of-fit of the residual model.

The complete model fitted the genetic variation of partial resistance better than the restricted model but was significant only for leaf resistance. Moreover, the relative precision of variance components estimates was quite low, except for additive variance. Additive variance estimates were larger in the complete model than in the restricted model. Homozygous dominance variance was as important as additive variance. The covariances between additive and homozygous dominance effects were negative except for lesion size.

Prediction of genetic advance

Broad-sense heritabilities ranged from 0.46 to 0.81 (Table 5). Partial resistance of hybrids was more heritable than partial resistance of lines only for leaf resistance and lesion density. Except for lesion size, genetic advance by direct varietal creation was higher by selecting between hybrids than between lines. Therefore, the best variety which could be directly derived from the base population was a hybrid for leaf resistance, panicle resistance and lesion density. Again with the exception of lesion size, heterosis between the best hybrids and the best lines was higher than mean heterosis estimated in the base population.

Narrow-sense heritability ranged from 0.34 to 0.74 on the basis of the test system (Table 6). DH recurrent

Table 3 Genetic variance among lines and hybrids for partial blast resistance in the field and in the greenhouse

Traits	Line variance	SE[a]	Hybrid variance	SE	Ratio
Field leaf resistance	0.0179	53	0.0406	38	2.26
Field panicle resistance	0.1054	45	0.1109	42	1.05
Greenhouse lesion density	0.0238	63	0.0704	44	2.96
Greenhouse lesion size	0.0667	40	0.0381	78	0.57

[a] Standard error is expressed in percentage of the variance estimate

Table 4 Genetic variance components for partial blast resistance in the field and in the greenhouse in the restricted and complete models

Traits	Restricted model					Complete model								
	Var A	SE[a]	Var D	SE	R^2[b]	Var A	SE	Var D	SE	Cov AD°	SE	Var D°	SE	R^2
Field leaf resistance	0.0169	21	−0.0042	117	0.66*	0.0459	32	−0.0041	119	−0.0295*	52	0.0495*	70	0.88*
Field panicle resistance	0.0377	26	−0.0074	244	0.44	0.1152	37	−0.0073	249	−0.0730	62	0.1012	110	0.66
Greenhouse lesion density	0.0238	29	0.0266	60	0.56*	0.0514	51	0.0266	60	−0.0324	83	0.0690	82	0.63
Greenhouse lesion size	0.0397	25	0.0185	104	0.61*	0.0309	51	0.0184	105	0.0032	543	0.0150	305	0.62

[a] Standard error of the variance component is in percentage of the variance estimate

[b] R^2: coefficient of determination of the least-square estimation of variance components, tested by Fisher's test ($0.05 < P < 0.15$)

Table 5 Broad-sense heritability and genetic advance for partial blast resistance by direct selection on line and hybrid values

Traits	Heritability[a]		Genetic advance[b]		Best hybrids/best lines[c] (%)
	Lines	Hybrids	Lines	Hybrids	
Field leaf resistance	0.46	0.74	0.242	0.461	23
Field panicle resistance	0.71	0.71	0.728	0.745	13
Greenhouse lesion density	0.49	0.81	0.286	0.634	19
Greenhouse lesion size	0.70	0.54	0.574	0.381	3

[a] Broad-sense heritabilities were calculated with the design variance for two repetitions

[b] Genetic advance was predicted with the design variances for two repetitions and a selection intensity of $i = 2.66$

[c] Best hybrids/best lines ratio was calculated from 1% best variety means

Table 6 Narrow-sense heritability and genetic advance by recurrent selection using three systems of test for line or hybrid values in the restricted model

Traits	Heritability[a]			Genetic advance for line or hybrid values		
	DH	*S*1[c]	GCA[c]	DH	*S*1[c]	GCA[c]
Field leaf resistance	0.67	0.52	0.41	0.249	62	39
Field panicle resistance	0.62	0.46	0.34	0.358	61	37
Greenhouse lesion density	0.69	0.46	0.44	0.299	58	40
Greenhouse lesion size	0.74	0.55	0.52	0.399	61	42

[a] Narrow-sense heritabilities were calculated with the variance components for two repetitions

[b] Genetic advance was calculated with the variance components for two repetitions and a selection intensity of $i = 1.65$

[c] *S*1 and GCA genetic advance were expressed in percentage of the DH genetic advance of each model

selection was the most efficient selection method by which to improve the blast resistance of the CNA-IRAT 5 population. Genetic advance using *S*1 families or GCA as a selection test was only half that reached with DH lines. The DH selection method was also the best procedure in the complete model. The superiority of hybrids versus pure lines after selection remained constant in the restricted model but increased in the complete one.

Indirect selection on resistance components

All components of partial resistance were positively correlated for hybrids and lines (Table 7). For example, lesion density and lesion size (Fig. 2), lesion density and field leaf resistance or panicle and leaf resistance were significantly correlated. Estimates of additive and dominance correlations were calculated in spite of their high imprecisions, showing, for instance, that additivity was mainly involved in the genetic relationship between greenhouse and field resistance.

Indirect selection on leaf resistance to improve panicle resistance was relatively efficient for both kinds of varieties compared to direct selection (Table 8). Indirect genetic advance on field leaf resistance with respect to the assessment of lesion size and lesion density in the greenhouse was predicted to be more than 50% of direct genetic advance. The efficiency of partial resistance breeding in the greenhouse in order to improve field panicle resistance was much lower. The combining of all resistance components as predictors did not increase the selection efficiency of field partial resistance to any great extent. In particular, lesion size and lesion density did not greatly improve the precision of field resistance assessment. Index selection on leaf and panicle resistance provided genetic gains on both traits jointly of the same magnitude as those reached by univariate direct selection.

Table 7 Genetic correlations[a] between partial resistance in the field and in the greenhouse for lines and hybrids

Traits	Field leaf resistance	Field panicle resistance	Greenhouse lesion density	Greenhouse lesion size
Field leaf resistance		0.47	0.43	0.79
Field panicle resistance	0.39		0.14	0.37
Greenhouse lesion density	0.41	0.46		0.59
Greenhouse lesion size	0.15	0.35	0.91	

[a] Correlations for lines and hybrids are below and above the diagonal, respectively

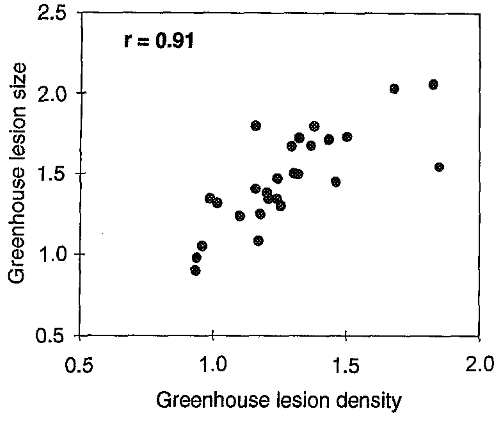

Fig. 2 Representation of the correlation between two components of partial blast resistance, lesion size and lesion density for inbred lines

Discussion

Existence of genetic variability for partial blast resistance

Partial resistance was considered to be a trait quantitatively inherited because the observed genetic variation could not be explained by simple genetic determinism. Moreover, lines and hybrids with genes for complete resistance to the inoculated isolate were clearly eliminated from the partial resistance analysis. Partial resistance must be controlled by a great number of minor genes, as observed by Wang et al. (1994) who detected a few quantitative trait loci. Its inheritance was quite different from that of the "quantitative resistance" defined by Ou (1980), which was only a function of the genes for complete resistance. However, we can not be absolutely sure that contamination of the field experiment with local blast races did not occur. While field partial resistance could have been confused in part with the expression of genes for complete resistance, no contamination has ever been reported in similar experiments (Notteghem 1985). Moreover, ECJ5P'88 belongs to the most frequent race in Goiânia (IB-9) and must have remained predominant at least until resistance assessment of the leaf.

Importance of additivity in the inheritance of blast resistance

Additive effects were preponderant in the determinism of partial resistance. In upland rice, Notteghem (1985) noted the importance of additivity in partial blast resistance. Geiger and Heun (1989) reported that quantitative resistance to fungal disease is mainly additive in most host-pathogen combinations. However, positive heterosis for blast resistance was detected for all components of partial blast resistance. Wang (1989) reported positive heterosis for blast resistance in three *indica* rice crosses. Conversely, in diallel analysis of upland rice, Notteghem (1985) observed negative heterosis in the greenhouse. Moreover, the genetic variance among hybrids was higher than the genetic variance among pure lines because of negative covariance between additive and homozygous dominance effects and, for greenhouse resistance, high dominance variance. Heterosis and higher variance among the hybrids led to the conclusion that hybrids will remain more resistant than pure lines after selection.

Such an organisation of the genetic variability can be observed only for low frequencies of favourable alleles with complete dominance in the hypothesis of biallelism (Gallais 1990). Breeding for partial blast resistance is a new breeding objective (Bonman 1992), and most of the parents of the CNA-IRAT 5 population have a low level of partial resistance (Veillet 1993). Furthermore, the CNA-IRAT 5 population is a broad-base population composed of *japonica* (87.5%) and *indica* (12.5%) alleles that must interact highly. In fact, CNA-IRAT 5 should be compared like other *indica-japonica* populations to an "unselected population", i.e. a population with a low frequency of favourable alleles, for most traits, especially grain yield (Veillet 1993). In an analysis of yield in alfalfa, Gallais (1977, 1984) observed a genetic variance in crossing that was higher than the variance among lines and interpreted this result in terms of allele frequency. In maize, the variance among lines is usually higher than the variance among single crosses (Gallais 1990). Cornelius and Dudley (1976), in an attempt to estimate the five components of variation in one maize synthetic, concluded that favourable alleles were at a high frequency for all of the traits studied.

Table 8 Genetic advance[a] on field partial resistance of lines and hybrids using five combinations of resistance components

Predictor traits	Field leaf resistance		Field panicle resistance	
	Lines	Hybrids	Lines	Hybrids
Field leaf resistance	100	100	31	48
Field panicle resistance	48	45	100	100
Greenhouse lesion size and density	51	68	39	33
All components of field and greenhouse resistance	106	103	101	102
Index[b] (field leaf resistance, field panicle resistance)	88	91	90	91

[a] Genetic advance was expressed in percentage of the direct univariate genetic advance

[b] Selection index on field leaf and panicle resistance using the inverse genetic standard deviation as economical weights

Genetic relationship between components of partial resistance

Field blast resistance has been broken down into leaf and panicle resistance. The genetic determinism of each component was slightly different even if positively correlated, as observed by a few authors (Bonman 1992). Rice breeders and plant pathologists should select jointly for panicle and leaf resistance using, for example, a selection index. Field experiments should be preferred to blast nurseries for partial resistance assessment, especially in order to estimate panicle resistance (Ou 1980). Leaf resistance was broken down into lesion density and lesion size, with both components being highly correlated, as has already been observed for a few cultivars (Villareal et al. 1981; Notteghem 1985; Roumen 1993). They could be used as indirect selection criteria for field resistance but with a moderate efficiency. Lesion density or lesion size would be necessary but not sufficient factors of field leaf resistance. Other components of partial resistance such as those related to the epidemiological development of blast disease, such as latent period, or to plant morphology, such as plant height (Veillet 1993), should be considered.

Heterosis for leaf resistance was much higher than heterosis for its components, lesion density and lesion size. Leaf resistance, estimated in the field by the diseased leaf area, is a multiplicative function of lesion density and lesion size. Heterosis for a multiplicative trait is usually higher than heterosis for its components (Schnell and Cockerham 1992). Dominance effects cannot explain heterosis for leaf resistance as dominance variance was not significant, even with non-transformed data. Multiplicative gene action is a source of epistasis, theoretically undetectable at the level of variance, which generates high levels of heterosis (Dillmann 1992). Panicle resistance was not clearly related with components of leaf resistance. It is a complex trait which can be broken down into a few components of resistance (Roumen 1993). The genetic analysis of their determinism should be undertaken.

Appendix 1 Genetic model relating variance components to genetic (co)variances

Genetic (co)variances	Components of variance			
	Var A	Var D	Cov AD°	Var D°
CgL(0)	1	0	2	1/2
CgL(1)	1/2	0	1	1/4
CgL(2)	1/2	0	1	1/4
CgS2	1	1/16	3/2	9/32
Cg(L,S2)	1	0	7/4	3/8
CgF	1/2	0	0	0
CgM	1/2	0	0	0
CgMF	0	1	0	0
Cg(L,GCA)	1	0	1	0

Breeding for durable blast resistance by recurrent selection

Selection for partial resistance by recurrent selection must be very efficient in this population. Recurrent selection should be more efficient than direct selection from the base population, as has been observed for other quantitative traits. Estimates of broad-sense and narrow-sense heritabilities were higher than those reported by Wang et al. (1989), which were calculated on a single-plant basis. These authors concluded that potential gains from mass selection would be slow because of high environmental variation. Yet, partial blast resistance of the CNA-IRAT 5 population increased significantly after three cycles of mass recurrent selection in the greenhouse in Brazil, showing that low heritabilities could be compensated for by high selection intensities (Filippi et al. 1992; Veillet 1993).

Nevertheless, partial resistance should be assessed in field experiments in family plots. Under these conditions DH selection should be the best strategy by which to improve the line and the single-cross values of the CNA-IRAT 5 population. We assumed for genetic advance prediction that anther culture was an efficient way to derive pure lines. If only a few differences were detected between DH and SSD lines derived from the CNA-IRAT 5 population, anther culture yield was very low and should be improved before wide-scale utilisation of haplo-diploidization (Veillet 1993). $S1$ selection should be therefore the most adequate breeding method, being both efficient to improve both hybrid and line values and practical for self-pollinated species. As $S1$ selection has been applied for 4 years in Brazil, the comparison of the realised genetic gain with the predicted one will provide interesting information on the reliability of genetic advance predictions.

Appendix 2 Expression of the phenotypic variance in test and the covariance between the test value and the line or the hybrid value for three recurrent selection scheme

Generations of test	Var T[a]	Cov TL[b]	Cov TC[c]
GCA	var $A/4$ + var $R/2$	var $A/4$ + cov $AD^\circ/4$	var $A/4$
$S1$	var A + var $D/4$ + cov AD° + var $D^\circ/8$ + var $R/2$	var $A/2$ + 3cov $AD^\circ/4$ + var $D^\circ/8$	var $A/2$ + cov $AD^\circ/4$
DH	2var A + 4cov AD° + var D° + var $R/2$	var A + 2cov AD° + var $D^\circ/2$	var A + cov AD°

[a] Var T = phenotypic variance in test

[b] Cov TL = covariance between the test value of a genotype and the line value of its offsprings after intercrossing

[c] Cov TL = covariance between the test value of a genotype and the hybrid value of its offsprings after intercrossing

Appendix 3 Genetic design variances and covariances estimated in the nested and factorial designs for partial blast resistance in the field and in the greenhouse (*Cg*, *Cr* genetic and residual (co)variances, respectively)

Traits	Genetic design (co)variances									Residual design variances		
	CgL(0)	CgL(1)	CgL(2)	CgS2	Cg(L,S2)	CgF	CgM	CgMF	Cg(L,GCA)	CrL	CrS2	CrH
Field leaf resistance	0.0096**	0.0138***	−0.0054	0.0217**	0.0126	0.0198***	0.0253***	−0.0045	0.0139	0.0418	0.0284	0.0286
Field panicle resistance	0.0086	0.0214	0.0754***	0.0180*	0.0005	0.0607**	0.0565**	−0.0063	0.0543	0.0857	0.0960	0.0921
Lesion density	0.0058*	0.0068	0.0112*	0.0643***	0.0128	0.0118	0.0345**	0.0241**	0.0058	0.0504	0.0438	0.0336
Lension size	0.0122*	0.0256	0.0290**	0.1011***	0.0338	0.0143	0.0091	0.0147	0.0136	0.0579	0.0479	0.0650

*,**,*** level of significance of the genetic effect, 15%, 5%, 1%, respectively, tested on the nested effect

In conclusion, our genetic study of the CNA-IRAT 5 population for partial resistance in the field and in the greenhouse showed that recurrent selection for blast resistance will be effective procedure by which to improve the line and single-cross values of the population. The predominance of additive gene action must not mask the importance of dominance and homozygous dominance in the determinism of partial resistance. In fact, hybrid breeding could be an alternative to pure line development to improve the blast resistance of upland rice cultivars. However, the relative resistance stability and durability of hybrids and lines remains to be assessed as significant host-pathogen interactions have been detected for partial blast resistance (Veillet 1993; Roumen 1993). Our interest of hybrid breeding therefore depends mainly on heterosis for yield, which has been evaluated to 60% of the line value in the CNA-IRAT 5 population (Veillet 1993).

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