Epidemiological Effect of Gene Deployment Strategies on Bacterial Blight of Rice

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ABSTRACT

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Experiments were conducted in farmers' fields at two locations of the irrigated lowlands of Laguna province in southern Luzon island, Philippines, during the wet seasons of 1993 and 1994. Nine rice populations were studied including pure stands, two-component mixtures, two-gene combinations of backcrossed lines containing varying combinations of the bacterial blight resistance genes *Xa-4*, *xa-5*, and *Xa-10*, and a non-isogenic cultivar containing *Xa-4* and partial resistance to bacterial

blight. The area under the disease progress curve (AUDPC) of both gene combinations studied was significantly less than the single most effective gene of each combination deployed singly. A mixture of a susceptible and a resistant line expressed an AUDPC significantly less than the mean of its component pure stands, but two other mixtures did not. The cultivar IR20, which contains both *Xa-4* and partial resistance, reduced the AUDPC by about two-thirds as compared with IR-BB4, which contains *Xa-4* and little or no partial resistance.

Additional keywords: *Oryza sativa*, *Xanthomonas oryzae* pv. *oryzae*.

Bacterial blight of rice (*Oryza sativa* L.), caused by *Xanthomonas oryzae* pv. *oryzae*, is a serious disease of global importance. No effective and economical chemical control methods are available (3). The major means of management is through the use of resistant cultivars. Eighteen bacterial blight resistance genes have been registered (12), and several resistance genes have been incorporated into agronomically suitable rice cultivars (29). However, gene-for-gene relationships have been suggested in the bacterial blight pathosystem (20,21,22,23). Deployment of simply inherited, uniform resistance over vast areas has decreased the effectiveness of resistance, because of selection for corresponding, virulent pathotypes (20,22,23).

Deployment methods to increase the durability of host plant resistance have often been discussed (13,19,24,33,37), but rarely have direct field comparisons been made of different deployment methods for a given disease. Information on gene deployment is largely lacking for the bacterial blight disease of rice (31). Thus, we conducted field experiments to determine the epidemiological effect of single genes, two-gene combinations, two-way mixtures of single-gene lines, and a line with partial resistance on the temporal progression of bacterial blight.

MATERIALS AND METHODS

Establishment of treatments. During the wet seasons of 1993 and 1994, identical experiments were conducted in Calauan and Mabitan in the irrigated lowlands of Laguna province in southern Luzon island, Philippines. Both locations are known to be endemic for high incidence of bacterial blight. Surveys conducted in

farmers' fields in 1992 (C. M. Vera-Cruz and M. R. Finckh, *unpublished data*) indicated that 97 and 40% of the isolates were virulent to both bacterial blight resistance genes *Xa-4* and *Xa-10* in Mabitan and Calauan, respectively. The remainder of the isolates were virulent on *Xa-4*, but not *Xa-10*. Virulence against *xa-5* was not detected in the surveys. The experiments were conducted in the same paddy in Mabitan in both years. However, in Calauan, the 1994 experiment was conducted in the paddy adjacent to the 1993 experiment.

The nine rice populations that were studied consisted of pure stands and mixtures of different rice genotypes (Table 1). Seven of these populations were pure stands, two-gene mixtures, and two-gene combinations of backcrossed lines containing varying assemblages of the bacterial blight resistance genes *Xa-4*, *xa-5*, and *Xa-10*. These lines were developed by backcrossing resistance sources four times to the recurrent parent IR24, which is susceptible to all known Philippine isolates of the pathogen (29). The remaining two populations were a pure stand and a mixture containing the cultivar IR20, which possesses the *Xa-4* major gene as well as a considerable level of partial resistance.

TABLE 1. Resistance genes of rice populations tested for their impact on epidemic development of bacterial blight in field experiments at two locations in the Philippines

Rice population	Resistance gene(s)
IR-BB4	<i>Xa-4</i>
IR-BB5	<i>xa-5</i>
IR-BB10	<i>Xa-10</i>
IR20	<i>Xa-4</i> and partial resistance
IR-BB4/5	Combination of <i>Xa-4</i> and <i>xa-5</i>
IR-BB4/10	Combination of <i>Xa-4</i> and <i>Xa-10</i>
IR-BB4 + IR-BB5	Mixture of <i>Xa-4</i> + <i>xa-5</i>
IR-BB4 + IR-BB10	Mixture of <i>Xa-4</i> + <i>Xa-10</i>
IR-BB5 + IR20	Mixture of <i>xa-5</i> + <i>Xa-4</i> and partial resistance

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While the 1993 trials were being conducted, it was found that only two-thirds of plants in our seed stocks of the IR-BB4/10 putative combination possessed both genes for resistance; the remaining plants possessed either one or neither of the two resistance genes. Seed stocks used in 1994 were breeding true for the presence of both resistance genes, as indicated by greenhouse inoculations.

In each location, the rice populations were grown in 4×4 -m plots in a randomized complete block design with four replications. A border of 4 m was planted between all plots with the cultivar IR48 in 1993 and IR54 in 1994, both of which provide some resistance against *X. oryzae* pv. *oryzae* races that can attack rice genotypes with resistance genes *Xa-4* and *Xa-10* (11).

Seedlings of all cultivars were grown in wet seed beds in a greenhouse for 3 to 4 weeks at the International Rice Research Institute. Seedlings were transplanted into field plots on 29 July 1993 and 22 July 1994 in Calauan, and on 5 August in both years in Mabitac. Surrounding fields were being planted by farmers at this time. Two to four seedlings per hill were transplanted, with 20 cm between hills. Mixtures were established by transplanting the same number of seedlings of each genotype in the same hill. The 1993 experiment in Calauan was lost to flooding and a subsequent invasion of the golden snail (*Pomacea* sp.) and was transplanted again on 6 September. Because of insufficient seed of IR-BB5, one replication in the 1993 Calauan experiment was without the

Fig. 1. Disease progress curves of bacterial blight on rice populations in farmers' fields at two locations in the Philippines. Table 1 has the description of the rice populations.

pure stand of IR-BB5 and the IR20 + IR-BB5 mixture. In both locations, missing hills due to snail and other damage were replaced with spare seedlings (mixtures) or by dividing hills within the plots (pure stands).

In Calauan, the plots were fertilized with 126 kg/ha each of N, P₂O₅, and K₂O. In Mabitac, the plots received 107, 13, 13, and 44 kg/ha of N, P₂O₅, K₂O, and S, respectively. Moluscacides and insecticides were applied as needed. When possible, golden snails were removed by hand until seedlings were established. Hand-weeding was performed two to three times per season.

Disease assessments. The experiments and the bordering fields were scouted weekly for the appearance of bacterial blight symptoms. Starting the week following the first appearance of disease symptoms (45 to 62 days after transplanting), disease severity was assessed weekly until the plants became too senescent to allow for reliable distinction of bacterial blight lesions (about 90 to 97 days after transplanting). An exception was at Calauan in 1993, when assessments were begun at 45 days after transplanting despite the earlier appearance of bacterial blight.

For disease assessments, 10 hills were picked randomly from each plot by reaching in blindly from the edge so as to avoid spreading the disease by walking inside the plots. Later in the epidemics, when virtually all hills showed infection, hills were also picked in the center. Each of two observers recorded the percent leaf area covered by bacterial blight lesion(s) for all leaves in five hills per plot. Means over 10 hills were calculated to give percent diseased leaf area per plot. The data were used to calculate the area under disease progress curve (AUDPC) for each plot, following Shaner and Finney (34).

Data analyses. AUDPC data were subjected to analyses of variance for a randomized complete block design using the General Linear Models Procedure (PROC GLM) of the Statistical Analysis System (SAS Institute Inc., Cary, NC). Sums of squares for host population were divided into eight preplanned linear contrasts. Lines with resistance gene combinations were contrasted with the most effective single gene contained in each of the two combinations to determine if there were interactions between the two genes for disease reaction. Each of the three mixtures was contrasted with the mean of its component pure stands to determine if mixing host genotypes resulted in altered epidemic development as compared with the components grown separately in pure stand.

Initial analyses of AUDPC data were conducted on individual experiments, as well as combined over locations and years, to determine the relative merit of conducting separate versus combined analyses. Exploratory analyses indicated heterogeneous variances that could not be corrected with standard transformations. Therefore, each datum was weighted by the inverse of the variance of its treatment mean, using the WEIGHT option of PROC GLM, to obtain the best linear unbiased estimators. Interactions of host population with location and year were all highly significant.

TABLE 2. Area under disease progress curve (percent days) for bacterial blight of rice on nine host populations grown in farmers' fields at two locations in the Philippines during the wet seasons of 1993 and 1994

Rice population ^a	Location				Grand mean
	Calauan		Mabitac		
	1993	1994	1993	1994	
IR-BB4	143.1	130.0	70.9	57.8	100.5
IR-BB5	15.3	0.0	0.6	0.1	4.1
IR-BB10	114.6	97.9	113.0	66.6	98.0
IR-BB4/5	4.7	0.2	0.5	0.01	1.3
IR-BB4/10	90.7	71.5	69.3	18.9	62.6
IR20	39.6	70.2	22.2	14.4	36.6
IR-BB4 + IR-BB5	66.3	40.9	26.5	8.3	35.6
IR-BB4 + IR-BB10	131.4	112.8	87.4	47.7	94.8
IR-BB5 + IR20	41.9	46.8	8.9	7.0	26.2

^a Table 1 has the description of the rice populations.

However, the mean square for each of these interactions was less than 10% of the mean square for the main effect of host population, which justifies the use of a combined analysis (9).

RESULTS

Disease. Isolates collected from within and around the experiments indicated that 90% or more of *X. oryzae* pv. *oryzae* isolates were virulent against both *Xa-4* and *Xa-10*, but not against *xa-5* (M. R. Finckh, unpublished data). Thus, our plots were exposed to a pathogen population consisting primarily of isolates with combined virulence against two of the resistance genes under study, but few or no isolates were virulent against rice genotypes possessing the third gene.

Disease began early and progressed steadily throughout the season in both years at Calauan. Because of the need to transplant a second time at Calauan in 1993, the surrounding commercial fields were already diseased at the time of transplanting, resulting in a higher level of disease at the time of the first assessment in comparison with the other three experiments (Fig. 1). At Mabitac, epidemics started later and initially progressed slower than at Calauan. Later in the season, however, epidemic progression became steeper at Mabitac than at Calauan (Fig. 1).

Effectiveness of the resistance gene deployment strategies varied (Tables 2 and 3). AUDPCs of both gene combinations were significantly less than the single most effective gene of each combination deployed singly in pure stand. Although stocks of our IR-BB4/10 combination in 1993 were impure, results were similar when pure stocks were used in 1994. Only one of three mixtures significantly reduced the AUDPC relative to the mean of the pure stand components. Resistance genes deployed in two-gene combinations resulted in significantly less disease than when the same two genes were deployed as two-component mixtures. IR20, which contains both *Xa-4* and partial resistance, reduced the AUDPC by about two-thirds as compared with IR-BB4, which contains *Xa-4* and little or no partial resistance.

DISCUSSION

Our experiments provided an opportunity to compare different resistance genes deployed in a similar genetic background as single genes, gene combinations, and mixtures in the same experiments. Our results suggest that, for bacterial blight, resistance gene combinations and some mixtures can increase the effectiveness of resistance genes. Gene combinations were more effective than mixtures for the limited number of populations tested in this study. The partial resistance of IR20 provided very significant disease reductions relative to IRBB-4. This result is based on only one partially resistant genotype, and this cultivar was not near-

TABLE 3. Significance of linear contrasts for area under disease progress curve (AUDPC, percent days) for bacterial blight on nine rice populations^a grown in farmers' fields at two locations in the Philippines during the wet seasons of 1993 and 1994

Linear contrast	AUDPC	P value
IR-BB4 vs. IR-BB10	100.5 vs. 98.0	0.7558
IR-BB4 + IR-BB10 mixture vs. mean of IR-BB4 and IR-BB10 pure stands	94.8 vs. 99.2	0.5393
IR-BB4/10 combination vs. IR-BB10 pure stand	62.6 vs. 98.0	0.0001
IR-BB4 + IR-BB5 mixture vs. mean of IR-BB4 and IR-BB5 pure stands	35.6 vs. 52.3	0.0020
IR-BB4 vs. IR20	100.5 vs. 36.6	0.0001
IR-BB5 + IR20 mixture vs. mean of IR-BB5 and IR20 pure stands	26.2 vs. 20.3	0.1429
IR-BB4/5 vs. IR-BB5	1.3 vs. 4.1	0.0412
Mean of IR-BB4 + IR-BB10 and IR-BB4 + IR-BB5 mixtures vs. mean of IR-BB4/10 and IR-BB4/5 combinations	60.5 vs. 32.0	0.0001

^a Table 1 has the description of the rice populations.

isogenic to the other genotypes included in the experiment. However, previous studies have indicated a substantial impact of partial resistance on epidemic development of bacterial blight of rice (11,14). Our study addressed the effects of resistance gene deployment on temporal epidemic progression only. In determining the most useful approaches to resistance gene deployment, ease of breeding and effect on pathogen evolution will ultimately need to be considered.

We had no reason to expect, a priori, that the resistance genes we studied would or would not interact favorably for disease control when combined in a single genotype. The existence of "residual effects" of resistance genes has, in general, been a controversial and difficult area of study (30). However, the fact that both gene combinations provided a positive synergism for disease reduction in our study indicates promise for the use of resistance gene combinations against bacterial blight of rice, as has been the case for wheat (*Triticum aestivum*) rusts (*Puccinia* spp.) (15,32,35). Interestingly, greenhouse inoculations of IR-BB4/10 with nine compatible bacterial blight isolates did not show a synergistic effect on lesion length of bacterial blight (38). Infection efficiency and latent period may be important determinants of rates of epidemic development, and are not necessarily accounted for by lesion length measurements.

These experiments identified different effects of three mixtures on bacterial blight severity. Reddy and Nayak (31) found significant reductions of bacterial blight severity in mixtures of a resistant and a susceptible rice genotype, as in our study when resistant (IR-BB5) and susceptible (IR-BB4) backcrossed rice lines were deployed in a 1:1 mixture. In contrast, the IR-BB4 + IR-BB10 mixture provided no reduction in the AUDPC. This mixture was ineffective probably because prevalent isolates in both locations and years were virulent against both IR-BB4 and IR-BB10, and genetic backgrounds of these two lines were very similar. The mixture containing an effective resistance gene (IR-BB5) and a genotype with partial resistance (IR20) did not reduce epidemic progression of bacterial blight relative to the mean of its component pure stands. Though the epidemiological interaction of partial resistance and mixtures has been shown to be complex (4,10,28), one might expect that partial resistance would complement the epidemiological effectiveness of host diversity. However, IR20 was noticeably taller and had greater leaf area in mixture than did IR-BB5. Thus, the proportion of IR20 in this mixture was significantly greater than 1:1, which would increase the overall disease severity level of the mixture. Further, plant competition can influence susceptibility of a genotype to disease (5,6), and such a competitive effect could also have played a role in the IR-BB5 + IR20 mixture, in which IR20 was more competitive than IR-BB5.

Mixtures provided less control of bacterial blight of rice than has been the case for some other diseases. Intraspecific host mixtures have been shown to provide greater disease reductions against wind-dispersed pathogens of small grains (2,25,26,36) than we found for bacterial blight, which is caused by a splash-dispersed pathogen. Splash dissemination results in steep dispersal gradients (8,18), increased autoinfection (27) and, hence, a reduction in the efficacy of mixtures for disease control (7,27). Further, diseases with large lesions, as is the case for bacterial blight of rice, are less effectively controlled by mixtures than are diseases with smaller lesions (16,17). Finally, we tested only two-way mixtures in this study, and increased disease control might be seen with more complex mixtures.

A significant level of bacterial blight developed on IR-BB5 and IR-BB4/5 in Calauan in 1993, suggesting that resistance gene *xa-5* is likely to "break down" once deployed on a large scale. Adhikari et al. (1) suggested the deployment of *xa-5* in southeast and north-east Asia, because the matching virulence had not been isolated from these regions. However, the effectiveness of the *xa-5* resistance gene might be jeopardized if deployed uniformly and extensively in these regions.

Our trials in farmers' fields showed the epidemiological value of deployment of a rice genotype with partial resistance, gene combinations, and a mixture of a resistant and a susceptible line against bacterial blight disease of rice. Therefore, additional options are available to plant breeders for management of genetic resistance to bacterial blight, even after individual genes have been "defeated" by the pathogen.

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