Progress of Bacterial Blight on Rice Cultivars Carrying Different *Xa* Genes for Resistance in the Field

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ABSTRACT

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Progress of bacterial blight of rice, caused by *Xanthomonas oryzae* pv. *oryzae*, was studied in the Philippines by planting six rice cultivars (IR24, IR36, IR54, IR60, IR64, and IR1695) carrying different *Xa* genes for resistance during the 1988 and 1990 seasons. Four epidemiological parameters, 1) disease incidence, 2) disease severity, 3) area under the disease progress curve (AUDPC), and 4) apparent infection rate (r), were used to rank rice cultivars' resistance to *X. o. oryzae*. The susceptible check IR24 and resistant check IR1695 differed greatly in reaction to *X. o. oryzae* in the field during the 2-yr study. In the field, IR36, IR54, IR60, and IR64 showed high levels of resistance to *X. o. oryzae* compared with IR24. The progress of bacterial blight on these cultivars was significantly lower than that on IR24 as measured by AUDPC. The differences in rate of disease progress between rice cultivars had an effect on grain yield, and the reductions in yields were positively correlated with AUDPC values. High disease severity values were observed in 1988 when rainfall was high. For most rice cultivars, AUDPC values were positively correlated with rainfall, indicating that this factor was influential to development of bacterial blight of rice.

Additional keywords: epidemiology, host resistance, *Oryza sativa*

Bacterial blight of rice (*Oryza sativa* L.), caused by *Xanthomonas oryzae* pv. *oryzae* (ex Ishiyama) Swings et al (23), has been considered a potential threat to rice production in Asia (12,13,18). Chemical control of the disease is neither feasible nor practical. Thus, the development of resistant cultivars is one of the most effective and environmentally sound means to control this disease. Breeding rice for resistance to bacterial blight has been extensively carried out at the International Rice Research Institute (IRRI), Philippines. Twenty-one genes for resistance have been identified and are currently used in rice-breeding programs (17). In the Philippines, high levels of resistance to *X. o. oryzae* were found in some IR rice cultivars. This resistance slowed bacterial blight epidemics in the farmers' fields (14). The major gene *Xa-4* seemed to result in a durable form of resistance (11), which has stabilized the population of the pathogen (14). Nevertheless, the level of resistance of IR rice cultivars to *X. o. oryzae* has not been characterized. Yet, information on the reaction to *X. o. oryzae* is necessary to understand the disease epidemiology and to use resistant cultivars for disease management (1,25). The objectives of this study were to examine the effects of rice cultivars on bacterial blight progress, to compare the level of resistance to *X. o. oryzae* in rice cultivars under field conditions, and to determine the effect of the disease on rice yield.

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MATERIALS AND METHODS

Experimental rice cultivars. Six rice cultivars developed at IRRI, IR24, IR36, IR54, IR60, IR64, and IR1695 (the latter was a line with adult plant resistance selected from a cross between BPI76*$_4$/Zenith), were chosen for the field experiments. Except for IR1695, all rice cultivars used in this study are full-season, high yielding, and widely grown in Southeast Asia. The cultivars, their maturity, and race-specific genes for resistance to *X. o. oryzae* are as follows: susceptible check IR24, 118 days after sowing (DAS), no specific resistance; IR36, 110, *Xa-4* gene; IR54, 120, *Xa-4* gene; IR60, 110, *Xa-4* gene; IR64, 115, *Xa-4* gene; and IR1695, 120, *Xa-3* gene. Rice seeds were treated with 0.1% benomyl before sowing.

Description of field experiments. Field experiments were conducted at the IRRI farm (lat. 14°11′ N; long. 121°15′ E; 15 m asl) during the 1988 and 1990 seasons. The site had clay soil with pH 6.8. For the last 5 yr, rice had been planted at the site. Plants were transplanted on 21 August 1988 and 15 July 1990. The golden snail (*Pomacea canaliculata*) was controlled by applying triphenyltin acetate at the rate of 1 kg a.i./ha after harrowing in 1988; in 1990, they were collected manually every morning. The symptoms of tungro virus disease were observed in some plots in 1988, and diseased hills were destroyed as soon as the symptoms were seen. Urea was applied at the rate of 180 kg/ha in three split doses; one-half was broadcast basally at transplanting, and the remaining half was top-dressed in two applications at the maximum tillering and before initiation of the panicles. Plots were regularly irrigated from 1 wk after transplanting. No fungicides were applied after transplanting in either year.

Inoculum and inoculation. Strain IRN987 was used in 1988, and PXO86 of race 2 was used in 1990. The inoculum was prepared in small bottles containing 100 ml of peptone sucrose agar (PSA) (18). The bottles were incubated at room temperature for 72 hr, and bacterial cells were collected by suspending them in 100 ml of distilled water per bottle. The bacterial cells were filtered through double-layer cheesecloth and collected in conical flasks. Inoculum was adjusted to about 10^8 cells per milliliter using a spectrophotometer. Seeds of each rice cultivar were sown in nursery beds. After 20 days, seedlings of uniform size were carefully uprooted, and soil particles were washed from the roots with tap water. The seedlings were spray inoculated with a bacterial suspension in the evening and transplanted in the plots following morning.

Experimental design and disease sampling. The experiment was arranged in a split-plot design with the inoculated treatment as main plot and the rice cultivar as subplot with four blocks (10). The total size of each subplot was 4 × 4 m. Rice cultivars were arranged randomly within each plot, and there were two plants per hill in a 20 × 20 cm spacing. Ten days after transplanting, a 1-m^2 nondestructive sampling area was designated at the center of each subplot. Two border rows on each side of the subplot were not sampled. Samples were obtained from an area between border rows but outside of the nondestructive area (approximately 3.6 × 3.6 m). From each subplot, 30 randomly selected hills were tagged and used for successive disease assessments. Plots were enclosed by an electric wire to prevent rodent damage. Disease incidence was expressed

as the number of diseased leaves per hill divided by total leaves per hill × 100. Disease incidence was visually estimated for each tagged hill (30 hills per experimental unit) at 10-day intervals starting on 19 September 1988 and 13 August 1990.

Estimates of disease severity were made 30 days after transplanting at 10-day intervals on 20 leaves on each of the 30 tagged hills from September to November 1988 and from August to October 1990. Disease severity was expressed as mean disease severity (percent leaf area diseased) for 20 leaves per hill. Measurements were taken from the corner of each subplot towards its center. There were four possible positions for sampling. The positions were aligned approximately with the compass points NE, SW, NW, and SE. For example, an NE sample began at the corner of each subplot from the northeast and towards the center. Leaves were sampled equally from lower to upper canopy until 20 leaves were sampled. Leaves with complete necrosis were considered to be defoliated and thus were not rated for disease severity. Disease severity was estimated seven times for each cultivar in both years. Progress curves for disease severity versus time were used to compare the levels of resistance of rice cultivars during bacterial blight progression. Disease progress curves were analyzed and compared by calculating the area under the curve (AUDPC) for each cultivar (22). AUDPC was calculated for each subplot and standardized by dividing by the number of days in the epidemic. Apparent infection rate (r), expressed in logit units per day, was calculated by first converting disease severity values to a proportion on a scale of 0–1 and then transforming the data to logit (26). Data obtained from individual hills of each experimental unit were averaged and used for statistical analyses. Analysis of variance (ANOVA) was used to determine differences among disease incidence, disease severity, AUDPC, and r. Duncan's multiple range test was used to determine whether significant ($P < 0.05$ or 0.01) differences existed among rice cultivars.

Yield loss. A check subplot (noninoculated) was established for each rice cultivar to estimate the effect of the disease on rice yield. At maturity, 25 hills from diseased and apparently healthy subplots were harvested from each of the four replications. Grains were air-dried and weighed, and grain yield per square meter was converted into metric ton per hectare at 14% moisture. The percent yield loss was calculated by using the following formula: % Yield loss = (Yield from healthy subplots − Yield from diseased subplots)/Yield from healthy subplots × 100. The correlations among the four epidemiological parameters (disease incidence, disease severity, AUDPC, and r) and yield loss were calculated.

Environmental factors. Weather factors such as minimum and maximum temperatures (C), relative humidity (%), and rainfall (cm) were continuously monitored for each year. These data were collected for the growing season from the weather station of the IRRI farm closest to the experimental site. Hygrothermograph readings served as partial backup units. Mean temperature was calculated by summing the minimum and maximum temperatures and then dividing by 2. The combined analyses of variance on environmental factors and AUDPC were computed using general linear models of the SAS statistical package (20). Pearson's correlation coefficients between environmental factors and AUDPC values for each rice cultivar were determined, and the possibility of obtaining significant correlation values was tested at the 1 and 5% level of significance.

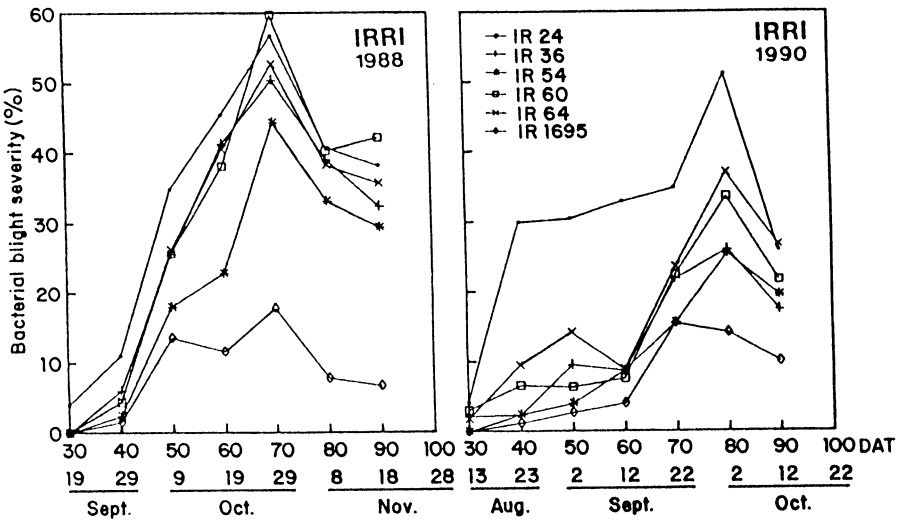

Fig. 1. Disease progress curves of the six rice cultivars infected with *Xanthomonas oryzae* pv. *oryzae* in the Philippines during the 1988 and 1990 seasons. From 20 to 25 hills were sampled per replication. Mean disease severity was calculated from seven disease scores. From 10 to 15 leaves per hill were assessed per replication at 10-day intervals after transplanting (DAT).

RESULTS

Disease progress curves. Disease progress curves of the six rice cultivars which were infected with *X. o. oryzae* are presented in Figure 1. Only very few diseased leaves were found during initial observations. The disease progress curves decreased late in the season. Bacterial blight was more severe in 1988 than in 1990. In both years, disease development was initially faster in susceptible IR24 than in other rice cultivars and

Table 1. Disease incidence (DI), disease severity (DS), area under the disease progress curve (AUDPC), and apparent infection rate (r) of bacterial blight on six rice cultivars in the Philippines during the 1988 and 1990 seasons

	DI (%)[w]		DS (%)[w]		AUDPC[x]		r[y]	
Cultivar	1988	1990	1988	1990	1988	1990	1988	1990
IR24	72.37 a[z]	23.00 a	57.37 ab	51.23 a	2,098.23 a	1,724.60 a	0.047 a	0.023 a
IR36	54.87 ab	10.23 bc	50.39 ab	25.97 bc	1,783.81 b	777.32 c	0.037 a	0.013 ab
IR54	36.95 b	7.00 c	44.38 b	25.34 bc	1,351.96 c	654.57 c	0.030 a	0.010 b
IR60	51.20 ab	11.24 b	59.58 a	33.68 b	1,888.97 ab	885.10 bc	0.043 a	0.013 ab
IR64	53.30 ab	12.53 b	52.68 ab	36.97 b	1,794.66 b	1,068.08 b	0.043 a	0.010 b
IR1695	11.62 c	5.00 d	17.71 c	14.02 c	552.75 d	421.93 d	0.033 a	0.007 b

[w] Assessed 60–70 days after transplanting.

[x] AUDPC = $\Sigma_{i=1}^{n} [(Y_{i+1} + Y_i)/2] [(T_{i+1} - T_i)]$, where Y_i = bacterial blight severity (in percent) at the ith observation, T_i = time in days at the ith observation, and n = total number of observations (seven).

[y] Estimated by the linear regression coefficient (b) of the logit transformation of disease proportion plotted against time in days.

[z] Within a column, means followed by the same letter are not significantly different at $P < 0.05$ according to Duncan's multiple range test. Data are means of four replications.

Table 2. Correlation coefficients among four epidemiological parameters, disease incidence (DI), disease severity (DS), area under the disease progress curve (AUDPC), and apparent infection rate (r), and yield loss (%) in the Philippines during the 1988 and 1990 seasons

Measure of resistance	Epidemiological parameters							
	DI[v] (%)		DS[w]		r[x]		AUDPC[y]	
	1988	1990	1988	1990	1988	1990	1988	1990
DI	1.00	1.00						
DS	0.78**[z]	0.85**	1.00	1.00				
r	0.19ns	0.63**	0.34ns	0.69**	1.00	1.00		
AUDPC	0.80**	0.85**	0.92**	0.92**	0.36ns	0.62**	1.00	1.00
Yield loss	0.69**	0.56*	0.50*	0.63**	0.20ns	0.71**	0.56*	0.50*

[v] Expressed as number of diseased leaves per hill.
[w] Expressed as percent leaf area diseased per hill.
[x] Calculated according to logistic model of Vanderplank (26).
[y] Calculated using proportion of tissue diseased (20).
[z] * And ** = F tests significant at $P < 0.05$ and 0.01.

increased rapidly 30 days after transplanting. Maximum disease severity was reached in IR24 between 50 and 70 days after transplanting. IR1695 had the lowest disease incidence compared with IR36, IR54, IR60, and IR64 in both years.

The four epidemiological parameters to quantify the effect of resistance on bacterial blight progression were calculated for each rice cultivar (Table 1). Disease incidence, disease severity, AUDPC, and r were significantly ($P < 0.05$) greater in susceptible IR24 than in other rice cultivars, with one exception. In 1988, IR60 was not significantly different from IR24 for the four disease parameters. Resistant cultivar IR1695 had the lowest disease incidence, disease severity, AUDPC, and r in both years. High correlations between disease severity and disease incidence, and also between disease severity and AUDPC were observed (Table 2). High correlations between r and other epidemiological parameters were demonstrated in 1990. Correlations among disease incidence, disease severity, AUDPC, and r were not significant ($P < 0.01$) in 1988.

Yield loss. Grain yield and percent yield reduction varied among rice cultivars (Table 3). Maximum yield reduction was observed in IR24, and minimum yield loss was observed in IR1695. Regardless of rice cultivar, greater yield reduction was observed during 1988 than in 1990. Significant ($P < 0.05$) correlations between epidemiological parameters, disease incidence, disease severity, and AUDPC and yield loss were demonstrated (Table 2).

Environmental conditions. Small temperature fluctuations were observed during the 2 yr of the field experiments (Fig. 2). Mean temperature (26–28 C) and relative humidity (76–80%) were similar during the 1988 and 1990 seasons, but the amount of rainfall received during these seasons differed. Total rainfall was 1,435 mm in 1988 and 1,060 mm in 1990 during the test period. Bacterial blight progression was highly correlated with the environmental factors in 1988. Highly significant ($P < 0.01$) correlation was demonstrated between AUDPC values and rainfall in 1990 (Table 4). The combined analyses of variance for AUDPC (used as a measure of disease progression) and the environmental factors indicated significant genotype–environment interaction ($R^2 = 0.93$) (Table 5).

Table 3. Grain yield (t/ha) and yield loss (%) of six rice cultivars grown in the Philippines during the 1988 and 1990 seasons

Cultivar	Grain yield (t/ha)[y]					
	1988			1990		
	Healthy	Diseased	Yield loss (%)	Healthy	Diseased	Yield loss (%)
IR24	4.72 a[z]	3.22 b	31.78 a[z]	4.46 a	3.97 bc	10.98 a
IR36	4.24 b	4.06 a	4.25 bc	3.98 bc	3.89 bc	2.26 c
IR54	4.47 ab	4.38 a	2.01 c	4.31 b	4.15 b	3.71 bc
IR60	4.62 ab	4.21 a	8.87 b	3.34 c	3.20 c	4.19 bc
IR64	4.47 ab	4.08 a	8.72 b	4.48 b	4.15 b	7.37 b
IR1695	4.48 ab	4.42 a	1.34 c	4.72 a	4.64 a	1.69 c

[y] The individual subplots were harvested, and data are means of four replications.
[z] Within a column, values followed by the same letter do not differ significantly ($P < 0.05$) according to Duncan's multiple range test.

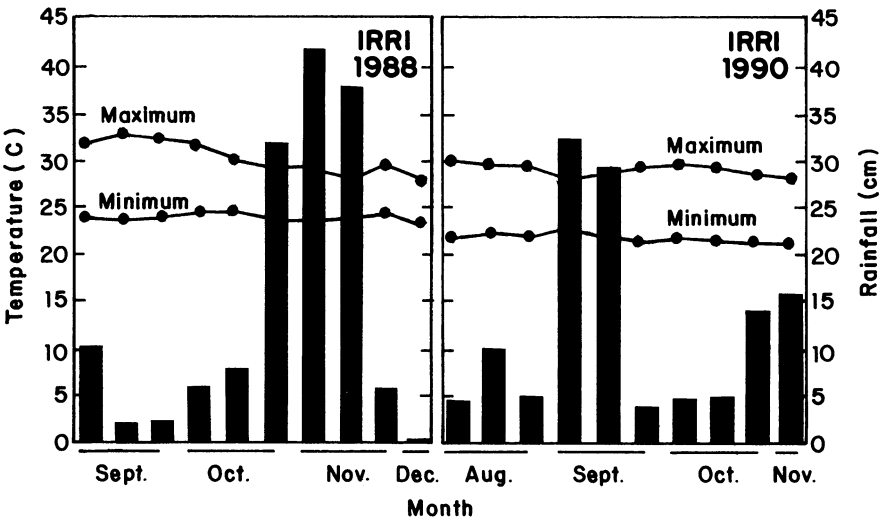

Fig. 2. Average minimum and maximum temperatures (C) and rainfall (cm) for selected months of the 1988 and 1990 seasons at the IRRI farm in the Philippines.

DISCUSSION

Differences among rice cultivars in relation to disease development were found under field conditions. IR36, IR54, IR60, and IR64 showed some partial resistance to *X. o. oryzae,* compared with susceptible check IR24. Because the progress of bacterial blight as measured by AUDPC was significantly ($P < 0.01$) lower on each of these four rice cultivars, IR36, IR54, IR60, and IR64, than on IR24, disease incidence could be used to provide quantitative information on bacterial blight development and to assess host resistance in the

field. Final disease incidence was often considered to represent the summation of host-pathogen-environment interactions over the course of a season (7,26,27, 30). Disease severity assessments may have limitations as means of detecting rice cultivar differences in the field. Using disease severity as a measure of resistance, differences between the fully susceptible rice cultivar IR24 and IR60 would not have been detected during the 1988 season. IR60 exhibited high disease severity values but sustained less disease than IR24 during the early part of season. The slower development of disease on IR60 was revealed by the AUDPC values, which measure the cumulative effects of resistance over the course of an entire season. Also, disease severity and AUDPC values were highly correlated in 1988 and 1990. Thus, in the 2-yr field study, AUDPC was the most reliable parameter for assessing resistance to *X. o. oryzae.*

These results agree with findings from other pathosystems (22,28). Apparent infection rate was not widely used to analyze bacterial blight development, possibly due to uncertainty regarding simple vs. compound interest disease (26). Diseases that progress by logistic growth were termed compound interest or polycyclic (26,30). Bacterial blight has been considered a systemic and vascular disease (14), and the logistic growth pattern of the disease progression could be similar to that of compound interest or polycyclic under a conducive environment. Host resistance in terms of its effect on the rate of disease development has been defined by r of the logistic model (2,4). In 1988, rates of disease increase on IR36, IR54, IR60, IR64, and IR1695 were found not significantly ($P < 0.01$) different from susceptible check IR24, despite having significantly lower disease incidence, disease severity, and AUDPC values. A fully susceptible cultivar IR24 exhibited the highest r in both years. However, high r can occur on cultivars with reduced disease levels when there is a rapid development of the disease within a short period of time. In some cases, this situation may augment experimental error and loss of conformation on the disease progress curve (22). This behavior also was observed in the present study, especially in rice cultivars IR60 and IR64. Likewise, the r values were not associated with disease severity and AUDPC in 1988. Thus, r may not be a reliable predictor to assess bacterial blight development on rice. This conclusion also was made by Berger (3), who reported considerable variation in the r during disease development. Similar findings were reported in slow-mildewing (22) and slow-rusting in wheat (28).

Significant ($P < 0.05$) differences in percent yield losses among rice cultivars were apparent. Resistant cultivar IR1695 had low yield reductions compared with susceptible check IR24. The range of yield reduction found in this study was comparable to those in other studies (8,19). Except IR1695, all rice cultivars used in this study were released to growers as commercial cultivars between 1970 and 1980. Despite a compatible reaction with race 2 of *X. o. oryzae,* all of these rice cultivars consistently exhibited low severities of bacterial blight in the Philippines. In addition, some of these IR cultivars were highly effective in reducing yield loss during severe epidemics in farmers' fields in the Philippines (14). Whether or not the resistance is quantitatively expressed to *X. o. oryzae* can only be determined from long-term field studies.

There was a significant genotype-environment interaction. Because identical bacterial strains were used and the same rice cultivars were grown in both years, environmental conditions appeared to be the factors that influenced disease development. The effect of gross environmental differences on bacterial blight development could be seen by comparing disease measurements in the two seasons. Weather conditions were generally more favorable for bacterial blight development in 1988 than in 1990, with high rainfall in late October and early November. In 1988, disease progression was highly correlated with temperature, relative humidity, and rainfall. A combination of weather factors interacted with each other, and a high inoculum resulted in higher disease levels for all rice cultivars in 1988. The high disease frequency in 1988 might have been due to conditions favorable for bacterial growth and multiplication. In fact, rainfall in 1990 was below normal during the reproductive stage of the crop. During the dry period, conditions for bacterial multiplication might not have been suitable, as infection was low and a slow increase in disease severity was found. Seasonal variations have been shown to influence the expression of resistance to fungal diseases of crop plants (5,6,21) as well as to bacterial blight (16,24). Significant ($P < 0.05$) to highly significant ($P < 0.01$) correlations between rainfall and AUDPC were observed in both years. This suggests that rainfall was the most influential factor for bacterial blight development in the tests. Fujikawa and co-workers (9) also reported correlation between disease development and rainfall and typhoons in the rice-growing season (15,24,29).

Future work needs to improve bacterial blight resistance of indica rices that are usually grown in the more productive areas in the tropics. These are areas of high rainfall and prolonged wet periods and are therefore more prone to bacterial

Table 4. Environmental factors which were correlated with area under the disease progress curve (AUDPC) in the Philippines during the 1988 and 1990 seasons

	Simple correlation coefficient (R^2)					
	Mean temperature (C)[y]		Rainfall (cm)		Relative humidity (%)	
Cultivar	1988	1990	1988	1990	1988	1990
IR24	0.89**[z]	0.26ns	0.77**	0.51*	0.62**	0.28ns
IR36	0.88**	0.10ns	0.76**	0.60**	0.52*	0.23ns
IR54	0.78**	0.06ns	0.64**	0.56*	0.52*	0.28ns
IR60	0.83**	0.11ns	0.70**	0.47*	0.55*	0.19ns
IR64	0.86**	0.14ns	0.73**	0.58*	0.57*	0.21ns
IR1695	0.93**	0.10ns	0.86**	0.43ns	0.66**	0.11ns

[y] Mean temperature = [(minimum + maximum temperature)/2].
[z] Level of significance: ns = F tests not significant at $P < 0.05$, * = significant at $P < 0.05$, and ** = significant at $P < 0.01$. All tests conducted during all growth stages, transplanting to harvesting of the crop.

Table 5. Combined analysis of variance of area under the disease progress curves (AUDPC)[v] and environmental factors using general linear model during the 1988 and 1990 seasons in the Philippines

Source of variance	df[w]	Sum of squares[x]	F values	R^2[y]
Year (E)	1	6134.30	168.86**[z]	0.93**
Genotype (G)	5	12470.98	68.66**	
G × E	5	1596.34	8.79**	
Time (T)	6	33382.64	153.16**	
G × T	30	3463.60	3.18**	
E × T	6	7007.52	32.15	
G × E × T	30	1994.84	1.83**	
CV (%)	30.35			

[v] Calculated according to Shaner and Finney (22) at 10-day intervals 30 days after transplanting. Time (T) = total observations of AUDPC, recorded seven times per year.
[w] Degrees of freedom.
[x] Combined analysis of variance conducted according to SAS package (20).
[y] Pooled coefficient of determination for both years.
[z] Level of significance: * = $P < 0.05$ and ** = $P < 0.01$.

blight outbreaks. In addition, the dense canopy architecture of the semidwarf rice cultivars may favor a prolonged period of free water on the leaf surface, thus providing an ideal environment for bacterial blight development. This necessitates characterization of leaf canopies at the microenvironment level. While this is a preliminary investigation on the effect of host resistance and environmental factors on bacterial blight development, more research should be initiated to analyze genotype–environment interaction in several locations so that this character can be efficiently and effectively manipulated in breeding programs.

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