# Identifying and Mapping a New Gene for Bacterial Blight Resistance in Rice Based on RFLP Markers

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## ABSTRACT

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Bacterial blight, caused by *Xanthomonas oryzae* pv. *oryzae*, is one of the most serious diseases of rice worldwide. We previously identified a rice cultivar, Zhachanglong, from Yunnan Province in southwest China that showed resistance to all 10 *X. oryzae* pv. *oryzae* strains tested. The objectives of the current study were to assess the identity of the gene in Zhachanglong and to determine the chromosomal location by restriction fragment length polymorphism (RFLP) mapping. We found that the resistance of Zhachanglong to bacterial blight is controlled by a dominant gene that is not allelic to *Xa1*, *Xa2*, *Xa4*, or *Xa14*. The new gene is linked to the *Xa4* locus, with a recombination frequency of 13.3 ± 4.5%. RFLP analysis resolved this gene to the end of the short arm of chromosome 11 in the rice linkage map, confirming the distinctness of this gene from all the known genes for bacterial blight resistance. We also found that this new gene is resistant to a broad range of *X. oryzae* pv. *oryzae* strains. We tentatively designated this gene as *Xa22*(t).

*Additional keywords*: broad-spectrum resistance, genetic analysis, *Oryza sativa*.

Bacterial blight, caused by *Xanthomonas oryzae* pv. *oryzae*, is a serious disease of rice worldwide (14). Developing resistant cultivars is generally considered the most effective and economical means of controlling this disease. A large number of studies conducted in several countries has identified 18 major genes with resistance to various races of the pathogen (7,15), which have been numbered in a series from *Xa1* to *Xa21*. In addition, there are several genes whose correspondence to the genes in the series have not been determined (9).

Considerable research effort also has been directed to utilizing the resistance genes in rice breeding programs (8). Such breeding efforts have resulted in a large number of cultivars and hybrids that carry various genes for bacterial blight resistance that have provided protection against the disease in many rice-producing areas of the world. However, as in many other host-pathogen systems, cultivars with newly incorporated resistance genes become susceptible after a few years of cultivation. For example, almost all the genes that have been employed in China have broken down and are no longer effective due to the emergence of new pathotypes (25,28). Thus, new genes for resistance are needed to combat bacterial blight.

Frequently utilized resources for new resistance genes include wild relatives of crop plants and germ plasm from centers of diversity. A recent example in rice of obtaining disease resistance from the wild relative is the *Xa21* gene from a wild rice, *Oryza longistaminata,* that exhibits a broad range of resistance against bacterial blight (7). Also, numerous disease resistance genes have been sampled from centers of diversity and incorporated into breeding programs for a large number of crop species (12).

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Yunnan Province in southwest China generally has been regarded as a center of origin as well as a center of diversity for Asian cultivated rice, *O. sativa* L. (16,24). In the search for new genes resistant to bacterial blight, Chen et al. (3) screened a total of 6,184 indigenous rice cultivars from Yunnan Province by inoculating each with 10 *X. oryzae* pv. *oryzae* strains obtained from China, Japan, and the Philippines. They found 345 cultivars that were resistant to at least 1 of the 10 strains. One *japonica* (*O. sativa* subsp. *japonica*) cultivar, Zhachanglong, exhibited resistance to all 10 *X. oryzae* pv. *oryzae* strains tested (Y. F. Xie, X. H. Lin, D. P. Zhang, Y. Chen, and G. Yu, *unpublished data*), showing great promise as a new source of bacterial blight resistance for rice cultivar development.

The study reported in this paper was undertaken: (i) to characterize the genetic basis of bacterial blight resistance in Zhachanglong; (ii) to assess the identity of the new gene by testing its allelism with previously reported bacterial blight resistance genes; and (iii) to determine the chromosomal location of this gene.

## MATERIALS AND METHODS

**Cultivars and populations for inheritance study and allelism test.** Two segregating populations were constructed to determine the inheritance of bacterial blight resistance: (i) an $F_2$ population derived from a cross between cvs. Zhachanglong and Zhenzhu Ai, an *indica* (*O. sativa* subsp. *indica*) cultivar that is susceptible to all *X. oryzae* pv. *oryzae* strains tested, and (ii) a backcross population ($BC_1F_1$) of Zhachanglong/Zhenzhu Ai//Zhenzhu Ai. The parents, $F_1$, $F_2$, and $BC_1F_1$, were grown in the bacterial blight disease nursery of Huazhong Agricultural University in Wuhan, China, during the rice growing season of 1992 and were inoculated with strain Pxo61 (*X. oryzae* pv. *oryzae* race 1 from the Philippines).

To test allelism between the gene in Zhachanglong and those characterized previously, we crossed Zhachanglong to four cultivars carrying known genes for bacterial blight resistance. These

cultivars included Kogyoku, which carries *Xa1* (19); Tetep, which carries *Xa2* (19); IR26, which carries *Xa4* (17); and TN1, which carries *Xa14* (22). The parents, $F_1$ and $F_2$ plants, were inoculated with the respective *X. oryzae* pv. *oryzae* strains used originally to identify the resistance genes (Table 1).

***X. oryzae* pv. *oryzae* strains, inoculum preparation, inoculation, and disease scoring.** A total of 17 *X. oryzae* pv. *oryzae* strains were used in this study (Table 2). Strains 72-67, HB17, JL691, Js49-6, Ks-6-6, LN42, LN44, OS75, and ZJ173 were from China (provided by Q. Zhang and L. Zhu). Strains Pxo61, Pxo79, Pxo71, Pxo112, and Pxo99 were from the Philippines (provided by T. W. Mew), and strains T7174, T7147, and T7133 were from Japan (provided by T. Ogawa).

For inoculum preparation, each of the bacterial strains was seeded on a potato semisynthetic agar medium (23) and incubated at 30°C for 3 days. Inoculum was prepared by suspending the bacterial culture with sterilized water to a concentration of about $6 \times 10^8$ cells per ml, measured by the barium sulfate turbidimetry method.

Rice seedlings were transplanted to the disease nursery 30 days after sowing. The space between plants in a row was 12 cm, and the rows were 24 cm apart. In all the experiments, the parents and $F_1$ populations were replicated twice, with 10 plants per replication. The $F_2$ and $BC_1F_1$ populations were tested on the basis of individual plants. At the booting stage (approximately 40 days after transplanting), five to seven of the uppermost fully expanded leaves of each plant were inoculated by the leaf clipping method (6), in which the leaf was cut with a pair of scissors predipped in the bacterial suspension.

For disease scoring, the longest lesion for each of two or three undamaged leaves per plant was measured 14 days after inoculation. A plant was classified as resistant if the average lesion length was ≤3.0 cm, moderately resistant if the lesion length was between 3.0 and 6.0 cm, moderately susceptible if the lesion length was between 6.0 and 9.0 cm, and susceptible if the lesion length was >9.0 cm. In the analyses, we combined the resistant and moderately resistant plants into the resistant class and the moderately susceptible and susceptible plants into the susceptible class.

**Restriction fragment length polymorphism (RFLP) assay.** The $F_2$ population between Zhachanglong and Zhenzhu Ai, tested with pathogen strain Pxo61, was used as the mapping population. DNA samples were prepared from fresh leaf tissue of field-grown $F_2$ plants by the method described previously (26). The bulked extremes approach (27) was followed to quickly locate the gene at its chromosome. A resistant bulk was made by mixing equal amounts of DNA from 30 highly resistant plants (lesion length shorter than 3 cm) in the $F_2$ population of 300 plants, and a susceptible bulk was made by mixing equal amounts of DNA from the 42 highly susceptible plants (lesion length longer than 9 cm). The DNA samples of the two parents and two bulks were digested with six restriction enzymes (*Bam*HI, *Dra*I, *Eco*RI, *Eco*RV, *Hin*dIII, and *Xba*I) and assayed for RFLP with 99 cloned fragments (provided by S. D. Tanksley's group [2] and the NIAR/STAFF [10]). DNA digestion, electrophoresis, blotting, and hybridization followed previously described procedures (18,26).

An additional sample of 121 plants taken at random from the same $F_2$ population was assayed with the markers that were likely to be linked to the bacterial blight resistance gene, as determined by the bulked extreme analysis. The location of the resistance gene on the RFLP linkage map was determined by Mapmaker/Exp 3.0 (11,13).

## RESULTS AND DISCUSSION

**Inheritance of bacterial blight resistance in Zhachanglong.** All the $F_1$ plants from the cross between cvs. Zhachanglong and Zhenzhu Ai were resistant to pathogen strain Pxo61 (data not shown). Segregation of resistant and susceptible plants (Fig. 1) fit a 3:1 ratio in the $F_2$ population ($\chi^2 = 0.84$, $P > 0.25$) and a 1:1 ratio in the $BC_1F_1$ population ($\chi^2 = 0.86$, $P > 0.25$). Thus, the bacterial blight resistance of Zhachanglong to Pxo61 was controlled by a single dominant gene.

**Allelism test.** If the resistance gene in Zhachanglong was allelic to a known gene for bacterial blight resistance, the resistance would not segregate in the progeny, and all the plants in the $F_2$ population would be resistant. On the other hand, if this gene was not allelic to a known gene for resistance, the plants in the $F_2$ population would segregate, and the segregation ratio would depend on whether these two loci are linked.

Thus, as can be seen in Table 1, none of the known genes included for the test (*Xa1*, *Xa2*, *Xa4*, and *Xa14*) were allelic to the

TABLE 1. Segregation of resistant and susceptible rice plants to *Xanthomonas oryzae* pv. *oryzae* in the $F_2$ populations of cv. Zhachanglong (ZCL) crossed to four different parents used for the allelism test

| Cross | Strain | Number of plants | | | Expected ratio | $\chi^2$ | *P* |
|---|---|---|---|---|---|---|---|
| | | Resistant | Susceptible | Total | | | |
| ZCL/Kogyoku (*Xa1*) | T7174 | 376 | 21 | 397 | 15:1 | 0.47 | 0.25–0.50 |
| ZCL/Tetep (*Xa2*) | T7174 | 316 | 18 | 334 | 15:1 | 0.29 | 0.50–0.75 |
| ZCL/IR26 (*Xa4*) | Pxo61 | 304 | 6 | 310 | 15:1 | 9.22 | <0.01 |
| ZCL/TN1 (*Xa14*) | Pxo112 | 476 | 31 | 507 | 15:1 | 0.02 | 0.90–0.95 |

TABLE 2. Description of the 17 *Xanthomonas oryzae* pv. *oryzae* strains used in this study and the reactions of rice cvs. Zhachanglong (ZCL), IRBB21, and Zhenzhu Ai (ZZA) to these strains

| | Strain[a] | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 72-67 | HB17 | JL691 | Js49-6 | Ks-6-6 | LN42 | LN44 | OS75 | ZJ173 | Pxo61 | Pxo79 | Pxo71 | Pxo112 | Pxo99 | T7133 | T7147 | T7174 |
| Origin[b] | Hun. | Heb. | Hub. | Hun. | Jiang. | Liaon. | Liaon. | Beij. | Zhej. | Phil. | Phil. | Phil. | Phil. | Phil. | Japan | Japan | Japan |
| Racial group | | II | | VII | II | | I | | IV | 1 | 3 | 4 | 5 | 6 | 3 | 2 | 1 |
| Reaction of cultivar[c] | | | | | | | | | | | | | | | | | |
| ZCL | R | R | R | MR | R | R | MR | R | MS | R | MR | R | R | R | MR | R | R |
| IRBB21 | MR | R | R | R | R | R | R | R | R | R | R | R | R | R | R | S | R |
| ZZA | S | S | S | S | S | S | S | S | S | S | S | S | S | S | S | S | S |

[a] The first nine strains in the table, 72-67 to ZJ173, were from seven different provinces in China. The racial groups of the Chinese strains were based on Fang et al. (4), the racial groups of the Philippine strains were according to Mew (14), and the racial groups of the Japanese strains were adopted from Horino (5).

[b] Hun. = Hunan; Heb. = Hebei; Jiang. = Jiangsu; Liaon. = Liaoning; Beij. = Beijing; Zhej. = Zhejiang; and Phil. = Philippines.

[c] R = resistant; MR = moderately resistant; MS = moderately susceptible; and S = susceptible.

resistance gene of Zhachanglong. It also is clear in Table 1 that three (*Xa1*, *Xa2*, and *Xa14*) of the four genes segregated independently of the gene in Zhachanglong. However, the segregation in the $F_2$ population from the cross between Zhachanglong and IR26 (*Xa4*) deviated highly significantly from the expected 15:1 ratio based on independent inheritance, indicating that the gene in Zhachanglong was linked to the *Xa4* locus. The recombination frequency, calculated by the maximum likelihood method (1), was 13.3 ± 4.5%.

To assess the possibility that the resistance of Zhachanglong to the various *X. oryzae* pv. *oryzae* strains was conditioned by more than one gene, we inoculated the plants in three of the four $F_2$ populations (Zhachanglong/Kogyoku, Zhachanglong/Tetep, and Zhachanglong/TN1) with a second *X. oryzae* pv. *oryzae* strain, JL691, that had different host ranges from those of T7174 and Pxo112. Approximately 97, 97, and 94% of plants in the three populations, respectively, expressed simultaneous resistant or susceptible reactions to both strains tested. Allowing for possible experimental errors in testing one strain or the other, this result indicated that the resistance of Zhachanglong to T7174, Pxo112, and JL691 was controlled by the same gene. For ease of description, we refer to the bacterial blight resistance gene of Zhachanglong as a new gene.

**Identifying the potential chromosomal region containing the new gene.** Of the 99 RFLP probes used in this study, 35 detected polymorphism between the two parents (Zhachanglong and Zhenzhu Ai). These 35 probes represented approximately 855 centimorgans (cM) (58%) of the RFLP linkage map (2). The polymorphic bands resolved by 29 of the 35 probes showed similar intensity in the resistant and susceptible bulks, indicating that these markers were not linked to the new resistance locus (27). Whereas, for the RFLPs detected by the remaining six probes (all from chromosome 11, listed in Table 3), the polymorphic bands from the susceptible parent were much more intense than those from the resistant parent in the susceptible bulk, indicating they were linked to the new resistance gene. We refer to these six markers as positive markers.

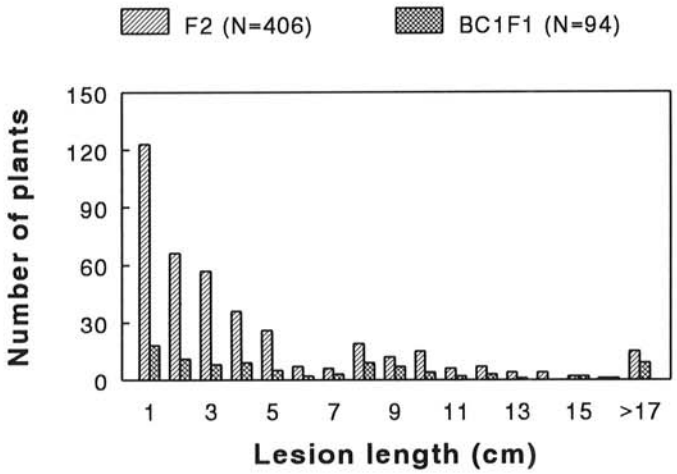


**Fig. 1.** Segregation of resistance to *Xanthomonas oryzae* pv. *oryzae* strain Pxo61 in the $F_2$ population of rice cultivar cross Zhachanglong/Zhenzhu Ai and the $BC_1F_1$ population of rice cultivar cross Zhachanglong/Zhenzhu Ai// Zhenzhu Ai.

TABLE 3. Calculation of map distances (in centimorgans) between the markers and the new gene for bacterial blight resistance with 42 highly susceptible rice plants

| Probe | Number of plants[a] | | | | $C^b \pm$ SE | Map distance (cM) |
|---|---|---|---|---|---|---|
| | 11 | 12 | 22 | Total | | |
| R543 | 1 | 4 | 37 | 42 | 7.1 ± 2.8 | 7.1 |
| RZ536 | 1 | 7 | 34 | 42 | 10.7 ± 3.4 | 10.9 |
| C950 | 1 | 9 | 32 | 42 | 13.1 ± 3.7 | 13.4 |
| G389 | 2 | 10 | 28 | 42 | 16.7 ± 4.1 | 17.4 |
| RG1109 | 3 | 17 | 22 | 42 | 27.4 ± 4.9 | 30.8 |
| G4001 | 3 | 17 | 22 | 42 | 27.4 ± 4.9 | 30.8 |

[a] Of the plants, 11 were homozygous for the bands from the resistant parent, 22 were homozygous for the bands from the susceptible parent, and 12 were heterozygous.

[b] $C$ = recombination frequency (percent).

**Determining the map location of the new gene with highly susceptible plants.** The recombination frequency ($C$) between a positive marker and the new gene locus was calculated by the formula given by Allard (1), assuming that all 42 susceptible plants were homozygous for the recessive allele at this locus. The distances between these markers (Table 3) agreed well with those given in the published maps (2,10). This analysis located the new gene locus at the end of chromosome 11, 7.1 cM from R543, which is on the short arm of this chromosome (20).

**Determining the map location of the new gene with a random population.** A total of 121 random plants from the same $F_2$ population was assayed for RFLPs with the six positive markers. An analysis by the Mapmaker program also located the new gene locus at the end of the short arm of chromosome 11 (Fig. 2). This chromosomal location is distinct from all the genes previously identified, including several loci mapped to the same chromosome (Fig. 2). Thus, mapping confirmed that the gene carried by Zhachanglong is a new gene for bacterial blight resistance.

However, chromosome 11 is the only chromosome with both ends mapped with telomere-associated sequences (10). The marker (R543) we found to be closest to the new gene is located only 1.9 cM from the telomere-associated sequence (TEL3) in the RFLP linkage map, whereas the new gene is mapped at a distance >7.0 cM from R543. This seems to suggest that the new locus is more distal than the telomere-associated sequence marker. Thus, the relative chromosomal locations of the new gene and TEL3 remain to be resolved. However, it is very clear that this new gene is located near the telomeric region of chromosome 11.

Another point is the relative efficiency of the susceptible class versus the random $F_2$ population in mapping the resistance gene.

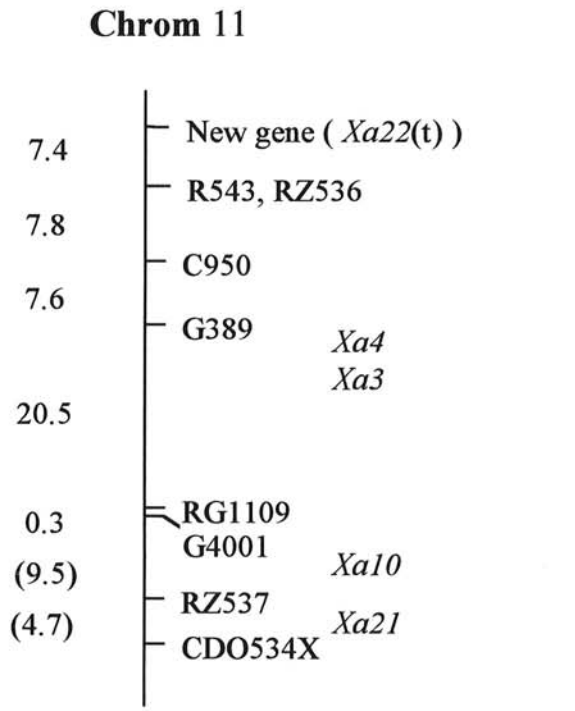


**Fig. 2.** The location of the new bacterial blight resistance gene, *Xa22*(t), in the restriction fragment length polymorphism (RFLP) linkage map. The locations of previously identified bacterial blight resistance genes (*Xa3*, *Xa4*, *Xa10*, and *Xa21*), the two accompanying RFLP markers (RZ537 and CDO534), and their map distances (in parentheses) are adapted from Causse et al. (2).

Zhang et al. (27) pointed out that efficiency of mapping with the recessive class is two to three times higher than with a random $F_2$ population per assayed plant. Also, it is likely that the disease scores of the extreme plants better reflect the genotype at the resistance locus than those with intermediate scores. Thus, the 42 highly susceptible plants may, in reality, contain more information for determining the map distance between RFLP markers and the new gene locus than the 121 random plants. However, we presented the mapping results based on the 121 random plants because there is no algorithm for map construction using data from the recessive class.

**The resistance spectrum of the new gene.** To evaluate the potential usefulness of this new gene in rice improvement, we tested the resistance of Zhachanglong against a total of 17 strains, representing a wide range of the bacterial blight pathogen, from China, Japan, and the Philippines. We also included cv. IRBB21, the carrier of *Xa21*, which possesses broad-spectrum resistance (7). Both cultivars showed resistance to 16 of the 17 strains inoculated (Table 2). However, these two cultivars differed in resistance to two strains: IRBB21 was susceptible to one of the Japanese strains, whereas Zhachanglong was susceptible to a Chinese strain. Thus, this new gene also has broad-spectrum resistance and may be an excellent source of bacterial blight resistance for rice cultivar development.

Eighteen genes for bacterial blight resistance have been identified, including *Xa21*, which has recently been isolated by map-based cloning (21). Because the gene from Zhachanglong appears to be distinct from all the known genes by allelism testing and by the chromosomal location, we tentatively designate this new gene as *Xa22*(t).

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