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Focus on Bacterial Blight of Rice

Bacterial blight of rice, caused by *Xanthomonas oryzae* pv. *oryzae* (37), was first reported in Japan over a century ago. Since then, considerable research on the disease and its causal agent has been reported and reviewed (18,19,24,29). In the past 10 years, advances in the area of molecular genetics, monoclonal antibody technology, and microbial taxonomy have been made. Now these technologies are being used to characterize the pathogen, reevaluate the ecology and epidemiology of the disease, and study host-parasite interactions. In this article, we will focus on the use and the potentials of these technologies to clarify the taxonomy of the pathogen, describe the pathogen population structure in single plants or fields, and investigate the molecular events occurring in the host-parasite interactions.

The Disease

Bacterial blight is found worldwide and is particularly destructive in Asia during the heavy rains of the monsoon season. In many Asian countries, bacterial blight has become endemic on rice following repeated cultivation. Reductions in rice yield may be as high as 50% in fields where the crop is severely infected (Fig. 1), and infection at the tillering stage can lead to total crop losses. More commonly, however, plants are affected at the maximum tillering stage, and yields are reduced 10–20% (29).

Bacterial blight is a vascular disease resulting in tannish gray to white lesions along the veins (Fig. 2). Under field conditions, symptoms usually are observed at the tillering stage; disease incidence increases with plant growth, peaking at the flowering stage (Fig. 3). A more severe form of the disease, kresek, may develop if roots or leaves are damaged and infected during transplanting at the seedling stage (Fig. 4). Infection at this stage usually results in seedling death 1–6 weeks after transplanting. Younger plants (less than 21 days old) are the most susceptible, and high temperatures (28–34 C) favor kresek development (23, 29,45).

In contrast to the bacterial blight pathogen, which enters leaves primarily through hydathodes, *X. o. oryzicola*, the causal agent of bacterial leaf streak, usually invades through stomata and enters xylem vessels only at late stages of infection, when multiplication is limited (H. Kaku, *personal communication*). Because of its infection of the mesophyll, *X. o. oryzicola* causes narrow, vein-delimited translucent lesions that later turn necrotic. Streak sometimes occurs on the same leaf with blight (Fig. 5) but can be distinguished from blight by the thinner, translucent lesions with yellow bacterial ooze.

The Pathogen

Advances in taxonomy. The bacterial nature of leaf blight was established by Japanese scientists in the early 1920s. The bacterium was originally named *Bacillus oryzae* Hori and Bokura 1911 and has been reclassified numerous times to include *Pseudomonas oryzae* Uyeda and Ishiyama 1922, *Bacterium oryzae* (Uyeda and Ishiyama) Nakata 1927, and *Xanthomonas oryzae* (Uyeda and Ishiyama) Dowson 1943. With the establishment of the pathovar system (6), the bacterial blight pathogen was reclassified as *X. campestris* pv. *oryzae*. The leaf streak pathogen, first described as a distinct organism in 1957 by Fang et al (7), then was classified as *X. c.* pv. *oryzicola* (6).

Van den Mooter (40) used numerical analysis of 295 phenotypic traits to show that *X. c. oryzae* was distinct from other *X. campestris* pathovars. Vera Cruz et al (42) and Kersters et al (16) demonstrated through phenotypic analysis and protein gel electrophoresis that strains of the bacterial blight pathogen constituted a homogeneous group, regardless of geographic origin. In addition, these features distinguished *X. c. oryzae* from *X. c. oryzicola*.

Using data from both classical and recently developed techniques for bacterial characterization, Swings et al (37) found that the leaf blight and streak pathogens were distinct from other *X. campestris* pathovars and proposed that they be reclassified as a separate species, *X. oryzae*, consisting of the pathovars *oryzae* and *oryzicola*. Fatty acid analysis (36), serological analysis with mono-

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clonal antibodies (3), and restriction fragment length polymorphism (RFLP) analysis with selected probes (17) also distinguished the two pathovars from each other as well as from other xanthomonads (Table 1).

Fig. 1. Rice field affected by bacterial blight.

Fig. 2. Bacterial blight of rice showing progression of symptoms from (left) mild to (right) severe.

Advances in detection and identification. Identification of *X. o. oryzae* using most of the aforementioned techniques requires pure cultures. However, the pathogen is not easily isolated because it grows slowly in culture relative to the numerous contaminants found on seed and plant materials (12). Thus, for detection of the pathogen in pure or mixed culture, serological methods provide a rapid and relatively sensitive solution.

The development of two pathovar-specific monoclonal antibodies (MAbs) for *X. o. oryzae* and *X. o. oryzicola* have unique applications in seed technology because they can distinguish strains of these pathovars from nonpathogenic xanthomonads (Table 1) that are prevalent on rice seed (3,11,14). Recovery of nonpathogenic xanthomonads on rice seed may lead to erroneous conclusions regarding the frequency of seed transmission of the bacterial blight pathogen unless the identity of *X. o. oryzae* is confirmed by pathogencity tests (21). Through repeated pathogenicity tests, it was found that nonpathogenic xanthomonads reacted only with genus-specific MAbs, X1 and X11, whereas *X. o. oryzae* strains reacted with these plus the pathovar-specific MAb *Xco*-1 (3). Likewise, *X. o. oryzicola* reacted with X1, X11, and the pathovar-specific MAb *Xccola*. With the immunofluorescent colony-staining technique developed by van Vuurde (41), *X. o. oryzae* can be distinguished from nonpathogens in rice seed extracts (Fig. 6).

In contrast to the pathovar-specific MAbs, DNA probes that hybridize only with DNA from *X. o. oryzae* have not yet been found. However, a repetitive DNA element cloned from *X. o. oryzae* can be used as a probe in RFLP analysis to differentiate *X. o. oryzae* from *X. o. oryzicola* and pathovars of *X. campestris* (17). All strains of *X. o. oryzae* tested from Asia, Australia, and South America contain many copies of the element (Fig. 7). The U.S. strains are exceptional in that DNA from these strains contain fewer copies of the repetitive element.

A panel of *X. o. oryzae* MAbs also distinguishes between North American and Asian strains (3). One MAb (*Xco*-5) was generated to a strain of *X. o. oryzae* isolated from the first outbreak of bacterial blight in the United States, which occurred in Texas and Louisiana in 1987. This MAb reacts to all strains from the United States but not to Asian, Australian, or South American strains. This MAb also reacts weakly with several strains of *X. o. oryzicola* from China and the Philippines. The U.S. strains thus have an epitope in common with *X. o. oryzicola*, and the MAbs indicate that the U.S. strains form a serological bridge between some strains of *X. o. oryzae* and *X. o. oryzicola*. The mild symptoms evoked by the U.S. strains on U.S. rice cultivars and the inability of the strains to induce symptoms on the IRRI differential rice cultivars are further indications of differences between the Asian and North American strains (3).

Diagnosis of races. A pathogen "race" is a group of strains (isolates) that evokes a particular combination of susceptible (compatible) and resistant (incompatible) reactions when tested on a standard set of differential host cultivars. Currently, nine races have been identified in the Philippines on the basis of reactions with the IRRI differential cultivars that contain resistance genes, namely, IR24 (0), IR20 (*Xa-4*), Cas 209 (*Xa-10*), IR1545-339 (*xa-5*), DV85 (*xa-5, Xa-7*), and TN1 (*Xa-14*) (18,43; R. Nelson, *personal communication*). Using these and other differential cultivars, many more races have been described from other geographic areas (see 18,28,43).

Subgroups of *X. o. oryzae* have been defined by differential reactions with panels of MAbs, by differences in the hybridization patterns of repetitive DNA probes, and by different fragment sizes produced after digestion with *Pst*I (J. E. Leach et al, *unpublished*; R. Nelson, *personal communication*). Neither MAbs nor DNA probes described so far are race-diagnostic but, rather, subdivide

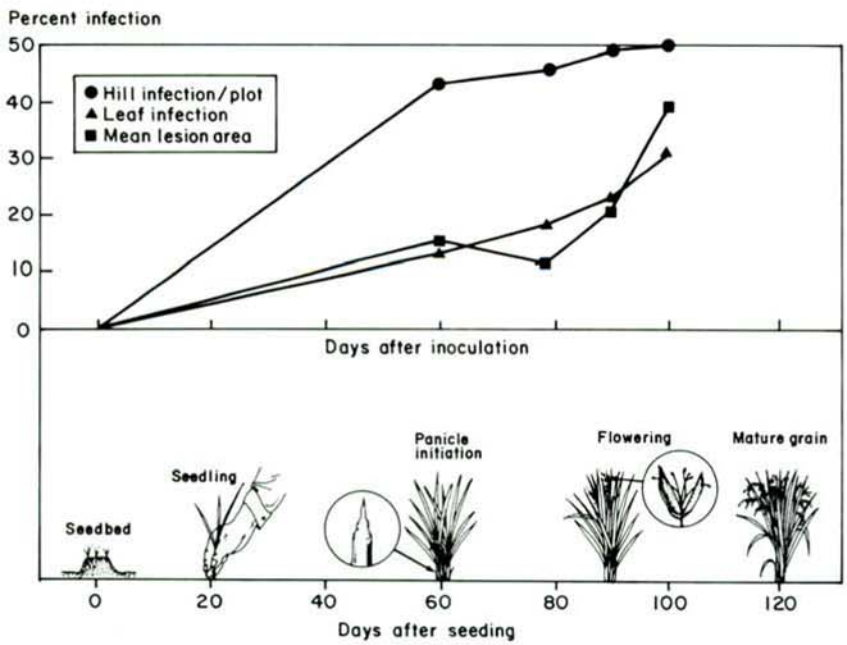

Fig. 3. Disease progress as related to stages of plant growth.

Fig. 4. Kresek symptoms on transplanted rice seedlings.

races. For example, 27 distinct RFLP types (unique patterns) were observed after hybridization with one DNA probe when 98 strains from six races of *X. o. oryzae* were tested (J. E. Leach et al, *unpublished*). The patterns thus subdivided the races, although some of the patterns may represent unique races. To determine if some distinct RFLP types are characteristic of races, Vera Cruz et al (44) inoculated strains of race 5 representing two different RFLP groups on 361 traditional rice accessions. The interactions with one rice accession differentiated the two RFLP types into races 5 and 7 of *X. o. oryzae*. Although it is unlikely that all RFLP types represent different races, the work of Vera Cruz et al (44) demonstrates the utility of RFLP for selecting strains likely to be genetically diverged and thus may be useful for identifying unrecognized resistance genes present in conserved germ plasm.

Fig. 5. Rice leaf with double infection: (left) narrow translucent lesions of bacterial leaf streak and (right) tannish gray lesion of bacterial blight.

Potential for analysis of pathogen population diversity. Traditionally, pathogen races are used as markers to assess population diversity because they have biological significance. Races of *X. o. oryzae* in populations have been monitored over time by inoculation to rice differential cultivars in Japan (27) and in the Philippines (22). In the Philippines, strains for the study were collected over time after the release in the early 1970s of modern, semidwarf rice cultivars carrying the bacterial blight resistance gene *Xa-4*. These cultivars accounted for over 90% of the total rice production in the Philippines by 1978. The predominant races in the population monitored over that time period changed such that within less than 10 years the prevalent races found were those that were virulent to cultivars containing *Xa-4* (22). Similar results were observed in Japan (27). Thus, both studies confirm accepted concepts in biotype selection, that is, the host cultivar genotype (presence of a resistance gene) can influence the genotype (race) of the pathogen population.

However informative, these studies do not indicate the genetic potential for population change because race may be a measure of only a few genetic traits. Further, the identification of new races is limited by the availability of cultivars with different resistance genes. For these reasons, race designation has a limited use in the measurement of genetic diversity of a population. Now, RFLPs, which measure the abundant variation in the DNA sequence, and MAb markers, which measure the variability of surface antigens, can be used to generate a large number of markers for more accurate assessment of genetic diversity in pathogen populations.

Studies that measure the genetic diversity in pathogen populations, while useful for understanding the potential for change, are all the more valuable if linked with studies that measure traits with biological significance such as race. For example, in a preliminary RFLP analysis of 98 strains collected in the Philippine Islands between 1972 and 1988 (the same time period as was monitored in the study by Mew et al [22]), it was found that the overall genetic diversity did not significantly change over time, that is, the variability of the pathogen population remained the same (J. E. Leach et al, *unpublished*). Thus, whereas the rice genotype influences the race structure of the pathogen population (22), a reduction in host diversity (by planting of cultivars with single resistance genes) does not result in a reduction in genetic diversity of the *X. o. oryzae* population as measured by RFLP typing using probe pJEL101.

The ability to characterize pathogen populations with greater detail will permit investigation into the impacts of host genotype, climate, and cropping intensity on variability of *X. o. oryzae*. For example, in the Philippines, rice ecosystems in the mountain and lowland areas differ in many respects. The mountain area has a temperate climate, and only one crop of mixed traditional rice cultivars is grown per year. In the tropical lowlands, two or three crops of modern semidwarf cultivars are grown. In the mountain area, only race 5 strains of *X. o. oryzae* are found, whereas other races, especially race 2, predominate in the lowland areas (18,22). Use of repetitive

Table 1. Comparisons between *Xanthomonas oryzae* pv. *oryzae* and *X. o.* pv. *oryzicola*

Characteristic	*X. o. oryzae*	*X. o. oryzicola*
Disease on rice	Bacterial blight	Bacterial leaf streak
Early symptoms	Water-soaking at margins of fully developed leaves	Fine translucent streaks along leaf veins
Phenotypic characteristics (Vera Cruz et al [42])		
Acetoin production	−	+
Growth on L-alanine as sole carbon source	−	+
Growth in presence of 0.001% cupric nitrate	+	−
Growth on 0.2% vitamin-free casamino acids	−	+
DNA-rDNA hybridization (Vera Cruz et al [42])	Both belong to second rRNA superfamily (sensu De Ley 1978)	
SDS-PAGE of cellular proteins (Kersters et al [16], Vera Cruz et al [42])	Both show similar banding patterns but each has unique bands	
DNA-DNA hybridization (Swings et al [37])	80% homology between pathovars	
Percent G + C of DNA (Vera Cruz et al [42])	64.6%	65.0%
Restriction fragment length polymorphism analysis (Leach et al [17])	Repetitive DNA probe from *X. o. oryzae* differentiates two pathovars: mismatch of bands between *X. o. oryzae* and *X. o. oryzicola*, 84–93%; between strains of *X. o. oryzae*, 8–36%; between strains of *X. o. oryzicola*, 8–69%	
Fatty acid analysis (Stead [36]; Yang and Swings, *unpublished*)	Fatty acid profiles similar but differences in presence of 12:0 3OH, 15:0 iso, 15:0 anteiso, 16:0 and 17:1 isoF fatty acids	
Serological analysis (Benedict et al [3])	Reacts with monoclonal antibody *Xco*-1 but not *Xccola*	Reacts with monoclonal antibody *Xccola* but not *Xco*-1

DNA probes that measure differences in the pathogen populations from the two areas (17; R. Nelson, *personal communication*) allows a more critical assessment of the relative significance of climatic and ecological factors on pathogen genotype.

Monitoring strains in epidemiological studies. For monitoring particular strains of a pathogen over time and space, an adequate means to detect and monitor the populations quickly is critical. Reporter genes, such as *lacZY* (5), that have been used to monitor other organisms might be used for *X. o. oryzae*, but only in locations where release of genetically engineered organisms is permitted. MAbs allow for rapid identification of wild-type organisms and can be used in simple assays such as ELISA. Thus, MAbs can be used to analyze the large numbers of samples required for epidemiological studies (1).

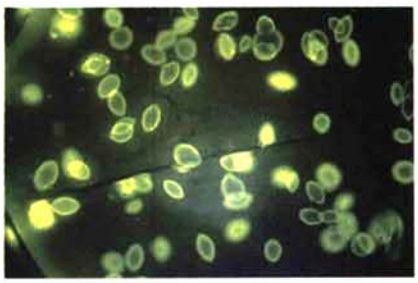

Fig. 6. Immunofluorescent ellipsoidal colony of *Xanthomonas oryzae* pv. *oryzae* treated with MAb *Xco*-1 within a dried and rehydrated 100-μl agar gel. (×40)

MAbs were used to map the distribution of two strains, PXO61 (race 1) and PXO86 (race 2), and to monitor disease progress under field conditions in the Philippines (35). As a second marker, clones selected for antibiotic resistance were employed to facilitate recovery on semiselective media. At the termination of two field trials, the race 1 strain predominated in all plots and appeared to have greater epidemic potential on a rice cultivar that lacked genes for resistance. To complement these studies, further analysis based on RFLP patterns of a smaller subset of the strains recovered from field samples is in progress (R. Nelson, *personal communication*).

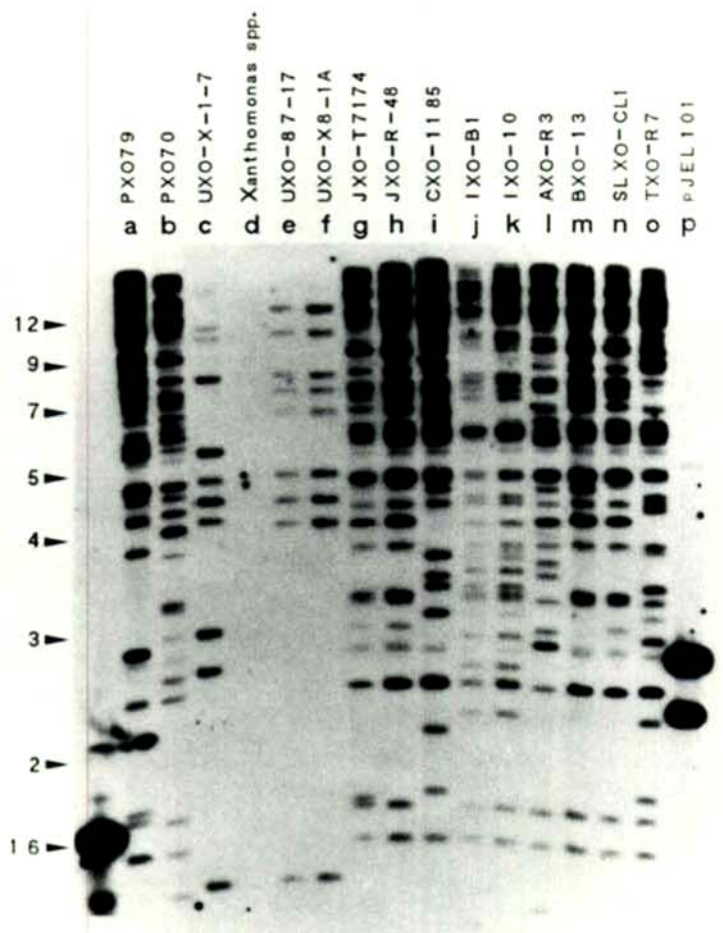

Fig. 7. Southern blot analysis of genomic DNA from strains of *Xanthomonas oryzae* pv. *oryzae* representing different geographic areas. The probe, a repetitive DNA element cloned from a Philippine strain of *X. o. oryzae*, reveals many differences among the strains. PXO79 and PXO70 are strains of races 3 and 4, respectively, from the Philippines; note the differences. Fewer bands of hybridized probe are observed with DNA of strains from the United States, designated UXO. There is no hybridization to a nonpathogenic strain of *Xanthomonas*. Although many bands are in common, considerable differences are apparent in the patterns of the strains from Japan (JXO), Colombia (CXO), India (IXO), Australia (AXO), Burma (BXO), Sri Lanka (SLXO), and Thailand (TXO). pJEL101 was digested with *Eco*RI and *Hin*dIII. Genomic DNA was digested with *Eco*RI.

Host-Parasite Interactions

X. o. oryzae is a vascular pathogen that enters vessels through wounds or through water pores of the hydathode (13). Hydathodes of rice consist of 10–20 water pores each and are densely distributed along the edge of the upper surface, predominantly near the leaf tips (20). After invasion of the water pore of a compatible host (Fig. 8), the pathogen multiplies in the epithem, a loose arrangement of parenchymatous cells and intercellular spaces beneath the water pores into which the xylem vessels open (38). After sufficient multiplication has taken place, bacteria enter the vascular system and block transpiration (Fig. 9). Exudation from hydathodes in the form of guttation droplets facilitates both ingress and egress of the pathogen (Fig. 10). The bacteria are not observed in the vascular sheath or in parenchymatous tissue, and although they have been observed in stomata, they apparently remain inactive and fail to multiply there (39; H. Kaku, *personal communication*).

Infection and multiplication in compatible and incompatible interactions. Multiplication and spread of *X. o. oryzae* have been monitored in rice leaves during compatible and incompatible interactions (2,15,25,30,31). Bacteria in both compatible and incompatible interactions spread from the inoculation point, but spread was faster in the compatible interactions. When the bacterial growth kinetics were measured in whole leaves using the same cultivars and strains, final numbers of bacteria in the incompatible interactions were 100- to 1,000-fold lower than those from compatible combinations (2).

Horino (9) used transmission electron microscopy to observe *X. o. oryzae* in rice leaf vessels during compatible and incompatible interactions. Three days after inoculation, bacterial cells within

Fig. 8. Cells of *Xanthomonas oryzae* pv. *oryzae* surrounding the water pore of a rice leaf.

vessels in incompatible interactions were irregular in shape and enveloped by abundant host-produced fibrillar material (Fig. 11). In contrast, bacterial cells in compatible combinations had normal morphology and were not surrounded by the fibrillar material until 20 days after inoculation (Fig. 12). Based on results of transmission electron microscopy studies, Horino and Kaku (10) suggested that the production of fibrillar material in vessels might be a postinfection defense mechanism.

Tissue specificity in infection and colonization. A detailed comparison of *X. o. oryzae* and *X. o. oryzicola* regarding infection sites and colonization prior to invasion may help to elucidate the mechanism of host resistance with respect to tissue specificity. Because both bacterial pathogens of rice can concomitantly infect the same leaf (Fig. 5), the *X. o. oryzae*/*oryzicola*-rice pathosystems offer a unique opportunity to initiate a course of comparative studies.

Biochemical characterization of resistance. Little is known about the molecular response of rice to *X. o. oryzae* in incompatible or compatible responses. Studies of the multiplication of *X. o. oryzae* in rice indicate that bacteriostasis occurs in incompatible interactions (2,15). Reimers and Leach (34) found that bacteriostasis was correlated with the early (24-hr postinoculation) accumulation of bright yellow-green autofluorescent compounds and host cell death in incompatible interactions (Fig. 13). In the compatible interactions, bacterial multiplication was not inhibited and host cell death and the accumulation of fluorescent compounds were not observed until late in the interaction (48 hr postinoculation).

Antibacterial compounds have been isolated from healthy leaves of susceptible and resistant rice cultivars (10) and from leaves after exposure to avirulent strains of *X. o. oryzae* (26). Some of the antibacterial compounds were oxidized lignin components with aldehyde and phenol groups (10). Reimers and Leach (34) demonstrated that during incompatible interactions, ligninlike polymers formed rapidly, whereas in compatible interactions, deposition of the polymers did not occur. The polymer deposition in the host cell was correlated with the accumulation of autofluorescent compounds, host cell death, a decrease in bacterial multiplication rates, and the onset of bacteriostasis in incompatible interactions.

Bacteriostasis and the deposition of ligninlike polymers also were correlated with an increase in the activity of an extracellular peroxidase during incompatible interactions (33). Peroxidases have been implicated in the last enzymatic step of lignin biosynthesis, that is, the oxidation of cinnamyl alcohols into free radical intermediates, which are polymerized into lignin. Because *X. o. oryzae* is found primarily in the vascular tissues and does not directly penetrate the host cell, it is unlikely that lignin itself serves as a physical barrier to pathogen spread. Perhaps the lignin biosynthetic process, which involves peroxidase activity, toxic phenolic compounds, and free radicals, is involved in the rice defense response against *X. o. oryzae*.

Genetic characterization of resistance. The existence of races of *X. o. oryzae* that are defined by patterns of incompatible and compatible reactions on rice cultivars with distinct resistance genes is evidence for gene-for-gene complementarity between the host and the pathogen. Recently, several avirulence genes have been cloned from *X. o. oryzae* (C. M. Hopkins and J. E. Leach, *unpublished*). The avirulence genes control bacterial elicitation of resistance only in rice cultivars carrying corresponding resistance genes (Fig. 14). Insertion of a transposable element within the avirulence genes disrupts their function and restores the virulence phenotype to strains harboring the element. The cloning of an avirulence gene from *X. o. oryzae* provides molecular genetic evidence that resistance in the interaction between *X. o. oryzae* and rice follows a gene-for-gene mechanism and provides a means to investigate physiological and biochemical mechanisms of resistance.

Prospects and Problems

Introduction of improved rice cultivars. Release of nitrogen-responsive rice cultivars in tropical Asia has unleashed the high epidemic potential of bacterial blight because cultivars were selected and planted without adequate disease resistance. This devastating bacterial disease subsequently has been a major biological constraint to increased rice production. Since the release of IR20, which carries the *Xa-4* gene for bacterial blight resistance, most of the improved rice cultivars that originate from the International Rice Research Institute carry that resistance gene. Although the deployment of resistant cultivars has proved cost-effective for control of this disease over the last decade, the emergence of virulent races has continued to be a constraint to rice production. The deployment of other resistance genes, such as *xa-5*, in breeding programs is desirable. Additional resistance genes continually are being sought for varietal improvement.

Successful development of varietal resistance depends on an adequate understanding of inherent variability as well as shifts in pathogen populations. Little information is available on this topic outside the Philippines and Japan. Knowledge of the type of resistance conditioned by a resistance gene is essential for maximal utilization of cultivars. Thus, the current challenge to plant pathologists, as well as plant breeders and molecular biologists, is both understanding the nature of variability and

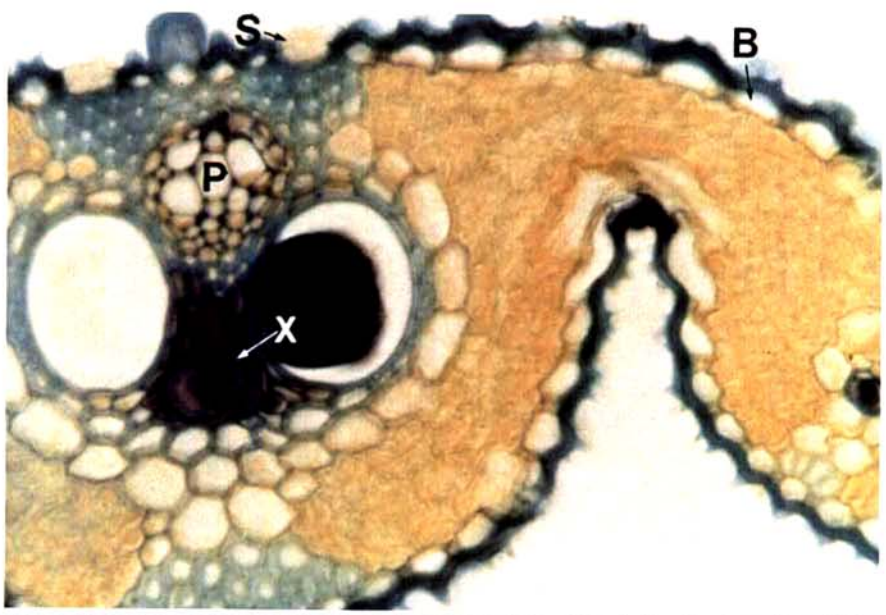

Fig. 9. Transverse section of rice leaf (adaxial surface at top) showing invasion of the xylem elements by *Xanthomonas oryzae* pv. *oryzae*. X = xylem, P = phloem, S = silica cell, B = bulliform cell. (Courtesy H. Kaku)

Fig. 10. Guttation from hydathodes of rice leaf.

assessing the performance of resistance genes in diverse rice ecosystems where bacterial blight remains a threat to rice production.

Alternative disease control strategies. Field sanitation, crop residue management, weed control, and perhaps clean seed all may enhance resistant cultivar control efforts, because rice stubble and weeds, such as *Leersia* spp. (7,8), are known to harbor the pathogen. However, effective management strategies cannot be designed unless the ecology of *X. o. oryzae* is properly documented. Although significant contributions have been made (4,11,32), information is lacking for many rice-growing areas.

Although *X. o. oryzae* is known to survive on rice hulls for several months after harvest, seed transmission of the pathogen to the subsequent crop is yet to be clearly demonstrated (21,24). In tropical environments, seedborne inoculum may be insignificant in comparison to inoculum carried over from successive cropping cycles. In temperate regions where crops are adequately fallowed, seed may be the primary inoculum source. However, this is speculation, because the impact of seedborne inoculum is unknown in either temperate or tropical zones.

Since genetic and serological markers for *X. o. oryzae* strains have been developed, the movement of wild-type strains can be traced through successive cropping cycles, and the disease potential of seedborne inoculum can now be investigated. Such studies should help to assess the cost efficiency of chemicals used for seed treatment, particularly in East Asia, where they are currently used. The impact on environments and induction of pathogen resistance should be assessed if chemicals are to be used on a wider scale.

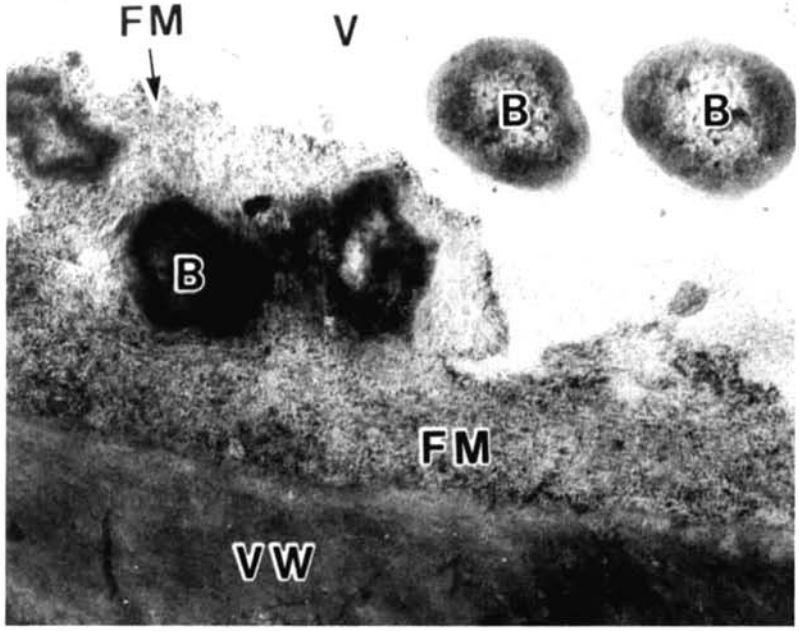

Fig. 11. Electron micrograph of bacterial infection in an incompatible interaction with rice. Bacterial cells (B) enveloped by fibrillar material (FM) were irregular in shape, and their cytoplasm became electron dense 3 days after inoculation. V = vessel, VW = vessel wall. (×16,500)

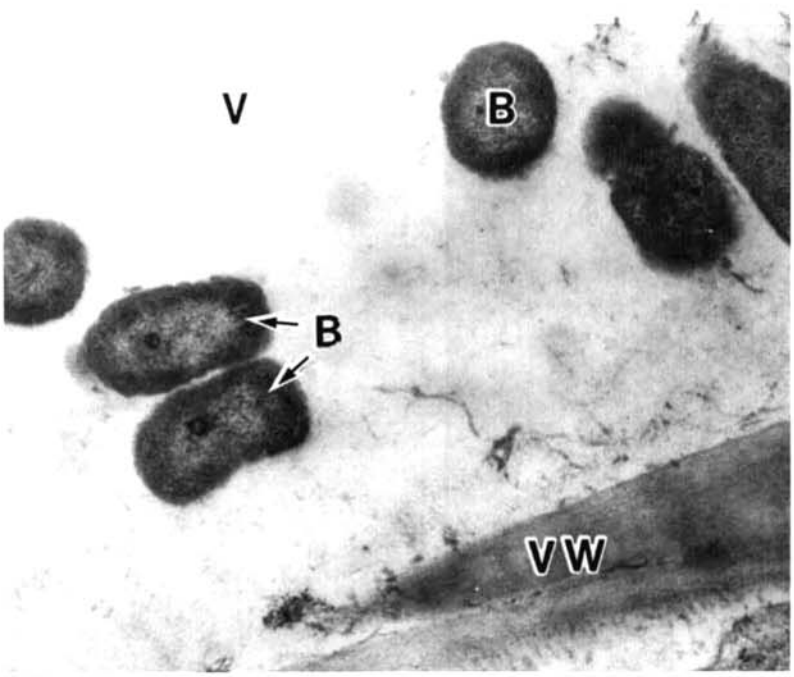

Fig. 12. Electron micrograph of bacterial infection in a compatible interaction with rice. No fibrillar material can be observed around the bacteria (B) in the vessel (V), and the bacteria appeared to reproduce actively 3 days after inoculation. VW = vessel wall. (×13,600)

Summary

Bacterial blight of rice is a disease of major significance throughout the world, and extensive literature is available on the pathogen and disease. The existence of defined races with consistent and measurable host reactions permit deeper investigation into the mechanisms of host resistance, and with the development of new molecular methods, bacterial blight has become an intriguing system for the study of host-parasite interactions. In addition, the new diagnostic methods that identify unique groups of strains within pathogenic populations can be used in the study of pathogen ecology, epidemiology, and control strategies. By use of serological and genetic probes in combination, great strides can be made into the understanding of population diversity and dynamics.

In the past 10 years, advances in the areas of taxonomy, molecular genetics, and monoclonal antibody technology have been made with *X. o. oryzae* and bacterial blight as the result of close collaboration among scientists from different laboratories. Further collaboration will be required to address the challenges outlined in this paper and to apply the information already attained to achieve effective disease assessment and control in the diverse rice ecosystems where bacterial blight remains a threat.

Acknowledgments

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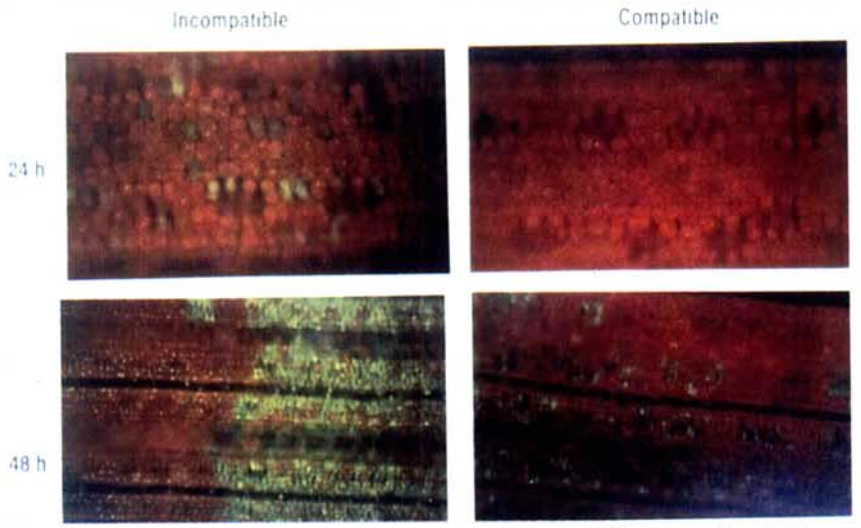

Fig. 13. Fluorescent micrographs of incompatible and compatible interactions between *Xanthomonas oryzae* pv. *oryzae* and rice at 24 and 48 hr after infiltration with bacterial suspensions. The red is autofluorescence of chlorophyll, characteristic of healthy, untreated tissues. In the incompatible interaction, numerous individual cells in the infiltration site fluoresced bright yellow-green within 24 hr, whereas in the compatible interaction, only red autofluorescence was observed until 48 hr after infiltration, when patches of yellow-green fluorescent cells were observed at the inoculation site.

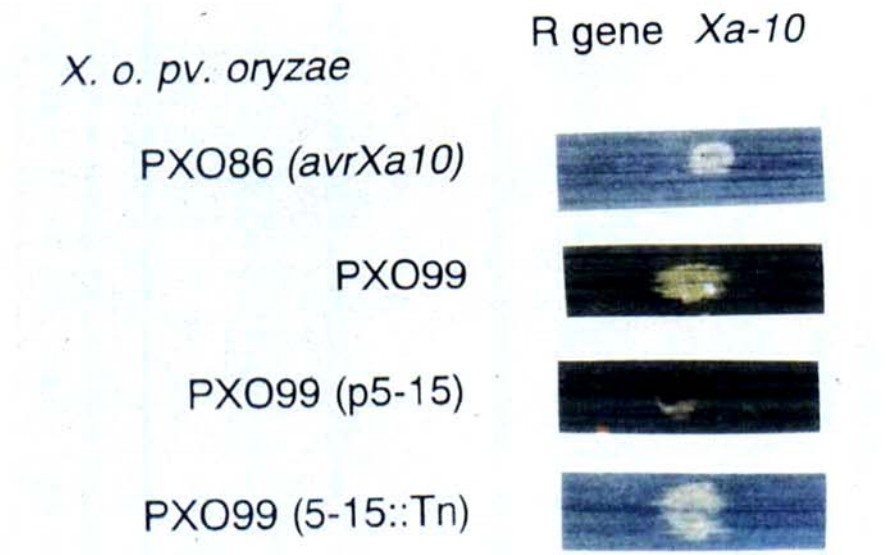

Fig. 14. Phenotypic interactions of rice cultivar IR-BB10, which contains the bacterial blight resistance gene *Xa-10*, with strains of *Xanthomonas oryzae* pv. *oryzae* PXO86 (race 2, avirulent to *Xa*-10), PXO99 (race 6, virulent), PXO99 with the cloned avirulence gene *avrXa10* (PXO99[p5-15], avirulent), and PXO99 with the Tn*5*-inactivated avirulence gene (PXO99[5-15::Tn], virulent).

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