



Bacterial Blight, a serious threat to productivity of rice (*Oryza Sativa* L.), an overview

Hamid Ali^{1*}, Fida Muhammad Abbasi¹, Habib Ahmad²

¹Department of Genetics, Hazara University Mansehra, Pakistan

²Islamia College University Peshawar, Pakistan

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Abstract

Xanthomonas oryzae pv. oryzae causes bacterial blight (BB) of rice (*Oryza sativa* L.), which constrain production of this staple crop in much of Asia and parts of Africa. Tremendous progress has been made in characterizing the disease and breeding for resistance. Bacterial blight is a vascular disease resulting in a systemic infection of rice and it produces tannish-grey to white lesions along the veins. In rice there are 38 major genes for resistance to bacterial blight and more than 30 races of *X. oryzae pv. oryzae* have been reported. Genetic resistance of rice to BB isolates is diverse as the pathogen exhibit significant diversity among the isolates. There is also a remarkable structural and functional diversity among genes for resistance to these isolates. This article review the recent advances and progress made towards the ultimate goal of developing disease-resistant varieties of rice. The objective of this review is to consolidate the existing knowledge about bacterial blight in rice and the progress made both in conventional as well as in molecular dimensions of breeding together with potential findings and constraints.

* Corresponding Author: Hamid Ali ✉ biotechd.ali@gmail.com

Introduction

Bacterial blight (BB) caused by *Xanthomonas oryzae* pv. *oryzae* (Xoo) is one of the most destructive diseases of rice. Rice is a worldwide staple as well as a model for cereal biology (Ronald and Leung, 2002; Shimamoto and Kyoizuka, 2002; Bennetzen and Ma, 2003). Xoo is important both from the standpoint of food security and as model for understanding fundamental aspects of bacterial interactions with plants. This article presents a brief review and a perspective on challenges for improved control of BB, and opportunities that the interactions of Xoo with rice present for advances in understanding of bacterial pathogenesis of plants and plant disease resistance.

Discovery and classification

Bacterial blight was reported for first time in Japan in 1884. It was originally believed to be caused by acidic soil (Ou, 1972). In 1909, masses of bacteria were isolated from the (acidic) turbid dewdrops of infected rice leaves, and the disease was reproduced by inoculating healthy leaves with these dewdrops. Shortly thereafter its etiology as a bacterial disease was established, and the causal agent was isolated and classified as *Bacillus oryzae* (Mizukami and Wakimoto, 1969). The bacterium was renamed *Pseudomonas oryzae* and later *Xanthomonas oryzae* (Ishiyama, 1922). In 1978, it was reclassified as *X. campestris* pv. *oryzae* (Dye, 1978). In 1990 the pathogen was elevated to its current status as a new species and named as *Xanthomonas oryzae* pv. *oryzae*. The species resides within the family Xanthomonadaceae in the Gammaproteobacteria (Swings *et al.*, 1990; Goto, 2012).

Morphology and physiology of Xoo

X. oryzae is a rod-shaped, round-ended, gram-negative bacteria. Individual cells ranges from 0.7 to 2.0 μm in length and 0.4 to 0.7 μm in width. The presence of a single polar flagellum make the cells motile. It forms round, convex, mucoid and yellow color colonies when grow on solid media. The yellow color is due to the production of a pigment xanthomonadin, which is a characteristic feature of the genus *Xanthomonas* (Bradbury, 1984).

The cells of *X. oryzae* produces numerous capsular extracellular polysaccharides (EPS). These EPS are important in the formation of droplets or strands of bacterial exudate from infected leaves, that provides protection from desiccation and are useful in wind- and rain-borne dispersal of pathogen (Ou, 1972; Swings *et al.*, 1990). It is aerobic and does not form spores. Optimal temperature for growth is 25 to 30 ° C. Like the genus as a whole, *X. oryzae* is catalase-positive, unable to reduce nitrate and a weak producer of acids from carbohydrates (Bradbury, 1984).

Distribution and impact

BB is endemic in Asia as well as in some parts of West Africa. It is prevalent in both tropical and temperate areas, and has also been reported in Australia, and Latin America (Mew *et al.*, 1993). In the United States, although an apparent mild outbreak of BB was reported in the late 1980s (Jones *et al.*, 1989), it was later determined that the bacterium associated with the disease was not Xoo (Ryba-White *et al.*, 1995). Confinements for Xoo exists in the United States and other rice-growing countries where the diseases are not endemic, but also in places where they are present, to prevent the introduction of new virulent strains. Implementation of biosecurity measures is an unfortunate necessity that somewhat restricts US research on this important pathogen of rice. Damage due to BB increased significantly following the widespread cultivation of high-yielding and nitrogen-responsive semi dwarf varieties of rice in early 1960s. Prior to the incorporation of resistant varieties and implementation of strict quarantine measures in Japan, BB damage was reported to ranges from 20 to 30% or as high as 50% (Ou, 1972). In tropical countries BB is even more destructive. Reports from the Philippines, Indonesia and India estimate that yield losses due to the kresiek syndrome of BB, which affects recently transplanted seedlings, have reached from 60–75%, depending on weather, location and variety of rice (Reddy *et al.*, 1979; Ou, 1985). In addition to reducing grain yield, BB may also affect grain quality by interfering with the process of grain maturation (Ou, 1985; Goto, 2012).

Mode of infection

Xoo enters the rice leaf typically through hydathodes at the leaf tip and leaf margin. Cells on the leaf surface may become suspended in guttation fluid as it exudes at night and enter the plant by swimming, or passively as the fluid is withdrawn into the leaf in the morning (Ou, 1985). Bacteria multiply in the intercellular spaces of the underlying epitheme, then enter and spread into the plant through the xylem vessels (Noda and Kaku, 1999). Xoo may also gain access to the xylem through wounds or openings caused by emerging roots at the base of the tillers (Ou, 1985). Within the xylem, Xoo presumably interacts with xylem parenchyma cells (Hilaire *et al.*, 2001). The pathogen moves vertically through the leaf through primary veins but also progresses laterally through commissural veins. Within a few days bacterial cells and EPS fill the xylem vessels and ooze out from hydathodes, forming beads or strands of exudate on the leaf surface, a characteristic sign of the disease and a source of secondary inoculum (Mew *et al.*, 1993). It may fall into irrigation water or be dispersed by wind, rain, insects or other means, and contribute to spread of the disease (Mew *et al.*, 1993; Nyvall, 1999).

Signs and symptoms

Bacterial blight is a vascular disease resulting in a systemic infection of rice (Mew, 1987) and it produces tannish-grey to white lesions along the veins. Symptoms are observed at the tillering stage, disease incidence increases with plant growth, peaking at the flowering stage (Mew *et al.*, 1993). There are two different phases of BB disease, the leaf blight phase and the kresek phase. Kresek is the most destructive manifestation of the disease, wherein the leaves of entire plant turn pale yellow and wilt during seedling to early tillering stage, resulting in partial or total crop failure. Young plants of less than 21 days old are most susceptible to kresek favored by temperatures between 28°C and 34°C (Mizukami and Wakimoto, 1969; Mew *et al.*, 1987). Leaf blight phase of BB has characteristic yellow lesions with wavy margins on leaf blades. The occurrence of bacterial ooze from infected leaves had been observed in warm and humid climates that contributed to spread of disease.

With passage of time, the lesion could cover the entire blade, which turned white and later grayish owing saprophytic growth (Ou, 1985).

Foliar symptoms of BB usually become evident at the tillering stage as small, green water-soaked spots at the tips and margins of fully developed leaves. The spots expand along the veins, merge, and become chlorotic and then necrotic, forming opaque, white to grey colored lesions that typically extend from the leaf tip down along the leaf veins and margins.

In the tropics, and particularly on susceptible cultivars of *O. sativa* ssp. *indica*, Xoo causes two disease syndromes with symptoms distinct from typical bacterial blight: kresek and pale yellow leaf (Nyvall, 1999). Kresek is a seedling blight that occurs shortly after transplant from nurseries to the field. The common practice of cutting leaf tips before transplanting plays an important role in the development of the syndrome. Cut leaves serve as an infection site for the pathogen, and after a few days, water soaked spots develop just beneath the cut tips. In addition, broken roots resulting from pulling seedlings off the seedbed serve as entry points for bacteria present in flood-irrigated fields. Bacteria spread through the vascular system to the growing point of the plant, infecting the base of other leaves, and killing entire plants in 2–3 weeks. Plants that survive kresek suffer arrested tiller growth, a stunted appearance and an overall yellowish green color (Nyvall, 1999; Goto, 2012). Pale-yellow leaf is observed in older plants and is sometimes considered a secondary effect of seedling leaf blight and wilt. Whereas older leaves appear green and healthy, younger leaves are uniformly pale yellow or whitish, and tillers do not grow fully (Mew *et al.*, 1993).

Sources of primary inoculum, dissemination and survival

Outbreaks of BB are more likely to occur during the monsoon season of the south-east Asian and Indian oceans (from June to September) than at other times of the year (Mew *et al.*, 1993). Wind and rain disseminate bacteria from infected rice plants and other hosts, as well as contaminated rice stubble from previous crop seasons—the most important sources of primary inoculum.

Severe epidemics often occur following typhoons, the fierce winds, wind-blown rain and hail of which both wound rice plants and disperse bacteria. Bacteria may also be disseminated in irrigation water (Nyvall, 1999), as well as by humans, insects and birds (Ou, 1985; Nyvall, 1999). Other hosts of Xoo include several species of wild rice (*O. nivora*, *O. rufipogon*, and *O. australiensis*) and a number of gramineous weeds (*Leersia oryzoides* and *Zizania latifolia* in temperate regions and *Leptochloa* spp. and *Cyperus* spp. in the tropics). In temperate regions, Xoo can survive the winter in the rhizosphere of weeds of the genera *Leersia* and *Zizania* as well as in the base of the stem and the roots of rice stubble (Mizukami and Wakimoto, 1969). In addition, in temperate regions, Xoo can survive in the soil for 1–3 months depending on the soil moisture and acidity, though this is not considered an important source of inoculum (Ou, 1985). Xoo can overwinter in piled straw as well; this source of inoculum may acquire importance in areas where little or no weedy hosts occur. In the tropics, high temperature, humidity and an abundance of host plants typically allow Xoo, to persist throughout the year (Ou, 1985). Xoo, can be isolated easily from seed of infected plants (Xie and Mew, 1998; Sakthivel *et al.*, 2001). Nevertheless, controversy exists over how long bacteria can survive in stored grain and whether seed-borne transmission is important.

Management of bacterial blight (BB) of rice

Control measures for management of BB include cultural practices, chemical and biological control, disease forecasting, and, most importantly, host genetic resistance, typically major gene resistance. Cultural practices useful for BB control vary depending on the location and disease incidence records. At the nursery stage, methods include seed disinfection, proper nursery drainage, and removal of diseased plants, weeds and debris. Prior to transplanting, fields may be disinfected by burning rice straw left from the previous season. Weeds are removed from canals and ridges in order to reduce natural habitats for the pathogen and its dispersal through irrigation water. At the paddy field stage, appropriate fertilization and proper plant spacing are the most recommended cultural methods of control (Mizukami and Wakimoto, 1969; Goto, 2012).

Fertilization must avoid an excess of nitrogen as it stimulates rapid vegetative growth of the plant, which favours disease development. Application of fertilizers rich in potassium and phosphorus, as well as application of agrochemicals at the maximum tillering to booting stages or after a typhoon or a severe flood are common practices (Mizukami and Wakimoto, 1969; Ho and Lim, 1979; Goto, 2012).

Chemical control

An ideal agent for chemical control should be one that functions at low concentration by either killing or inhibiting the multiplication of the pathogen or by blocking its important metabolic pathway. It should also readily translocate and be stable in the plant system and cause minimal damage to the environment. Attempts to control BB through chemicals like Bordeaux mixture with or without sugar, copper–soap mixture, and copper–mercury fungicides were made. Spraying copper oxychloride and streptomycin solution at short intervals was recommended to control this disease (Mizukami and Wakimoto, 1969). Chlorinating irrigation water with stable bleaching powder was also reported to be effective in minimizing the disease (Chand *et al.*, 1980). Chemical control of BB in rice fields began in the 1950s with the preventative application of Bordeaux mixture (hydrated lime and copper sulfate) and the testing of several antibiotics, mercuric and copper compounds. Laboratory tests determined that streptomycin derivatives and mercuric compounds were most effective, but they were found to damage rice grains when sprayed at the heading stage in the field (Mizukami and Wakimoto, 1969). In the 1960s, different kinds of agrochemicals were developed from repeated field trials and made available on a large commercial scale, mostly in Japan. They were based on L-chloramphenicol, nickel dimethyl dithio carbamate, dithianon and fentiazon. Most were unreliable, however, owing to variability in sensitivity among the pathogen population (Mizukami and Wakimoto, 1969; Ou, 1973). Although seed transmission of the disease is an uncertain source of primary inoculum, disinfection of rice seeds with mercuric compounds, antibiotic solutions or hot water is practiced in several countries in tropical Asia.

In temperate regions, chemical control of BB in nurseries and paddy fields includes the application of probenazole to the paddy water before and after transplanting the seedlings, in order to inhibit bacterial multiplication and prevent or retard the disease. Other chemicals such as tecloftalam, phenazine oxide and nickel dimethyl dithio carbamate are sprayed directly on plants (Mizukami and Wakimoto, 1969; Goto, 2012). However, chemical control of BB in the tropical monsoon climate of Asia is impractical, and no truly effective bactericide is commercially available for disease control (Lee *et al.*, 2003).

Biological control

Biological control is an environmentally friendly and cost effective alternative to chemical control. Bacterial antagonists of Xoo have received particular attention as biocontrol candidates, largely because of their rapid growth, easy handling and effective colonization of the rhizosphere (Vasudevan *et al.*, 2002). In India, about 40 bacterial isolates antagonistic to Xoo were identified through plate and field assays. Among those antagonists' native strains of the rice-associated rhizobacteria, *Pseudomonas fluorescens* and *P. putida* strain V14i (also used in biocontrol of the rice sheath blight pathogen, *Rhizoctonia solani*) significantly suppressed BB severity when sprayed on leaves (Sivamani *et al.*, 1987). For both agents, there was a significant correlation between endophytic survival in rice tissues and the extent of disease suppression (Johri *et al.*, 2003). Similarly, different species of *Bacillus* have been employed as seed treatment before sowing, root dips prior to transplanting and foliar sprays in the fields. In at least one study, BB was suppressed by almost 60%, and plant height and grain yield increased by two-fold (Vasudevan *et al.*, 2002). Although the mechanisms of BB suppression are not known, a recent investigation of biocontrol of the rice sheath blight disease has suggested that a rice systemic resistance response to the agents may be involved, as has been observed in other systems (Vasudevan *et al.*, 2002). Despite promising results such as these, biological agents have not seen widespread use in the control of BB.

Disease forecasting

Forecasting of BB is difficult because epidemics are dependent on the rice cultivars and cultural practices in use, in addition to environmental and geographical conditions. Methods used for forecasting may include inspection for early disease development and tracking climatic conditions (Mizukami and Wakimoto, 1969). In temperate locations, monitoring of bacteriophage strains specific for Xoo has been used in forecasting since the 1960s. Under particular agro environmental conditions, an increase of bacteriophage population in irrigation water and paddy fields early in the planting season correlates well with an increase in bacterial populations and is used to predict BB outbreaks. However, the bacteriophage forecasting system is not practiced extensively in tropical Asia, because rice cultivation is mostly rainfed, limiting the use of phage detection in paddy fields (Wakimoto and Mew, 1979; Murty and Devadath, 1982). In general also, disease forecasting has been of limited utility because chemical control is unavailable or impractical.

Genetic host resistance

Planting resistant cultivars has been the major method of BB management. Breeding and deployment of resistant cultivars carrying major resistance (R) genes has been the most effective approach to controlling BB. To date, 38 R genes to BB have been identified (see Table 1 for details and references), mostly from *O. sativa* ssp. indica cultivars, but some also from japonica varieties, and from related wild species including *O. longistaminata*, *O. rufipogon*, *O. minuta* and *O. officinalis* (Brar and Khush, 1997; Lee *et al.*, 2003). In addition, several resistance genes or alleles have been produced by mutating cultivated rice lines, e.g. by treatment with N-methyl-N-nitrosourea or thermal neutron irradiation, or by soma clonal mutagenesis (Gao *et al.*, 2001; Lee *et al.*, 2003). Some R genes are effective only in adult plants (e.g. Xa21) whereas most do not seem to be developmentally regulated (e.g. Xa23, Xa26). Curiously, Xa3 is typically effective only in adult plants, but against at least one race it is effective at all stages of growth.

Some genes condition resistance to a wide spectrum of Xoo races (e.g. Xa21, Xa23), whereas others are effective against only one or a few races that may be limited to a particular geographical location (e.g. Xa1). Most R genes to BB are dominant, but some are recessive (e.g. xa5, xa13), and some display semi dominance (e.g. Xa4, Xa27). Among the handful of genes that have been cloned there is remarkable structural diversity.

Most R genes to BB have been introgressed into the background of the susceptible indica cultivar IR24 to develop a set of near isogenic lines (NILs), and some have been pyramided, either through classical breeding and marker-assisted selection or through genetic engineering, to develop new plant types and NILs (Sanchez *et al.*, 2000; Singh *et al.*, 2001; Narayanan *et al.*, 2002).

Table 1. Genes conferring resistance to bacterial blight (BB) in rice.

Gene identified	Source of resistance	Reference
Xa1	Kogyoku	Yoshimura <i>et al.</i> , (1998)
Xa2	Tetep	He <i>et al.</i> , (2006)
Xa3	Wase Aikoku 3	Sun <i>et al.</i> , (2004)
Xa4	TKM 6	Wang <i>et al.</i> , (2001)
xa5	Aus Boro lines	Iyer and McCouch (2004)
Xa6	–	Sidhu <i>et al.</i> , (1978)
Xa7	DV85	Porter <i>et al.</i> , (2003)
xa8	PI231129	Singh <i>et al.</i> , (2002)
xa9	–	Ogawa <i>et al.</i> , (1988)
Xa10	Cas 209	Kurata and Yamazaki (2006)
Xa11	IR8, IR944	Kurata and Yamazaki (2006)
Xa12	Kogyoku	Oryzabase (2006)
xa13	BJ1 (Aus Boro)	Chu <i>et al.</i> , (2006)
Xa14	TN1	Kurata and Yamazaki (2006)
xa15	M41, mutant line	Nakai <i>et al.</i> , (1988)
Xa16	Tetep	Kurata and Yamazaki (2006)
Xa17	Asominori	Kurata and Yamazaki (2006)
Xa18	IR24, Toyonishiki	Liu <i>et al.</i> , (2004)
xa19	XM5	Kurata and Yamazaki (2006)
xa20	XM6	Kurata and Yamazaki (2006) ;
Xa21	<i>O. longistaminata</i>	Song <i>et al.</i> , (1995)
Xa22(t)	Zhachanglong	Sun <i>et al.</i> , (2004)
Xa23	<i>O. rufipogon</i>	Zhang <i>et al.</i> , (1998), (2001)
xa24	Aus 295	Lee <i>et al.</i> , (2000)
Xa25(t)	HX-3	Liu <i>et al.</i> , (2011)
xa26(t)	Minghui 63	Lee <i>et al.</i> , (2003)
Xa27(t)	<i>O. minuta</i>	Gu <i>et al.</i> , (2004), (2005)
xa28(t)	Lota Sail	Lee <i>et al.</i> , (2003)
Xa29(t)	<i>O. officinalis</i>	Tan <i>et al.</i> , (2004)
Xa30(t)	<i>O. nivara</i>	Cheema <i>et al.</i> , (2008)
Xa31(t)	Zhachanglong	Wang <i>et al.</i> , (2009)
xa32(t)	<i>O. meyeriana</i>	Zheng <i>et al.</i> , (2009)
Xa33	<i>O. nivara</i>	Natrajkumar <i>et al.</i> , (2012)
xa33(t)	Ba7	Korinsak <i>et al.</i> , (2009)
xa34(t)	Indica	Chen <i>et al.</i> , (2011)
Xa35(t)	<i>O. minuta</i>	SiBin <i>et al.</i> , (2010)
Xa36(t)	C4059	Lili <i>et al.</i> , (2010)
Xa38	<i>O. nivara</i>	Bhasin <i>et al.</i> , (2012)

Gene pyramiding

Pyramid lines have displayed higher levels and/or wider spectra of resistance to BB than the parental NILs with single R genes, suggesting synergism and complementation among R genes (Huang *et al.*, 1997; Narayanan *et al.*, 2002). Huang *et al.*, (1997) used gene specific PCR markers for the identification of pyramided line carrying different combinations of BB resistant genes. They obtained lines with different combination of genes, 2 lines for *Xa4/xa5/xa13*, 3 lines for *Xa4/xa5/xa21*, 3 lines for *Xa4/xa13/Xa21*, 3 lines for *xa5/xa13/Xa21* and 2 lines with all four genes (*Xa4/xa5/xa13/Xa21*). They also observed that *xa5* in any combination showed resistance against six BB Philippine races. With pyramid lines, it is possible to conduct quantitative analysis on the effect of each gene and their interactions, but most importantly, to maximize the performance and durability of genetic resistance. Resistance of rice to specific Xoo races is governed by both major R genes with a qualitative effect that condition complete resistance (CR) and polygenes with a quantitative effect (quantitative trait loci, QTL) that condition partial resistance (PR) (Li *et al.*, 2006). A recent study of the epistatic effects between R genes and QTL for resistance in rice revealed a complex genetic network in which the interactions between alleles at the rice R loci and alleles at the corresponding avirulence loci in Xoo lead to CR, and interactions between rice QTL for resistance and corresponding aggressiveness loci in Xoo lead to PR. Race specificity of the QTLs during PR and strong genetic overlap between CR and PR suggested that PR is essentially a 'weaker' CR (Li *et al.*, 2006). The distinction between CR and PR may be masked by the fact that some QTLs for BB may in fact be 'defeated' dominant R genes, or, in a sense, R genes that have lost their qualitative nature and adopted new, intermediate phenotypes (Li *et al.*, 1999). An example is *Xa4*, a single dominant gene for resistance to BB widely used in Asian rice breeding programs. *Xa4* conferred durable resistance in cultivars IR20 and IR64, among others developed at IRRI, before being overcome by the emergence of two new Chinese races in the early 1970s (Mew *et al.*, 1992).

The breakdown of *Xa4*- mediated resistance was manifested by significant changes in the qualitative action of *Xa4* (i.e. loss of dominance) and by a quantitative reduction of ~50% in the magnitude of the effect of the *Xa4* gene (Li *et al.*, 1999). However, the defeated *Xa4* can still act as a recessive QTL and show quantitative complementation when pyramided with other resistance genes in elite cultivar breeding. This complementation results partially from residual effects of the defeated *Xa4* against the new virulent Xoo races and partially from its epistatic/additive effects with undefeated R genes (Li *et al.*, 2001; Narayanan *et al.*, 2002).

Diversity among Xoo isolates

BB is characterized by a high degree of race–cultivar specificity. There are over 30 reported races of isolates from several countries (Mew, 1987; Noda *et al.*, 1996, 2001). A set of races identified in the Philippines using five differential rice cultivars (Mew, 1987) has been used widely for identifying and classifying resistance to BB in other cultivars (Ogawa *et al.*, 1991; Lee *et al.*, 2003). It has been noted, however, that screening for resistance to pathogen populations specific to particular geographical locations and tailoring regional breeding programs accordingly are important (Mew, 1987). Xoo also has a high degree of genetic diversity among different isolates, based on RFLP and pathotypes analysis of more than 300 strains from different parts of Asia, using a repetitive insertion sequence (IS) element as the RFLP probe (Adhikari *et al.*, 1995). In this study, isolates formed five clusters, each with more than one pathotypes. Some correlation of clusters with geographical distribution and specific pathotypes (races) was observed, indicating that tailoring breeding programs for specific regions is indeed a tenable approach to control, although there was also evidence of movement of strains among regions.

Evaluation of rice germplasm against Xoo isolates

Kaur *et al.* (2005) evaluated 125 accessions of rice of *Oryza nivara* against six Xoo Pathotypes prevalent in Punjab state of India over a period of three years and a few accessions showed resistance to all pathotypes.

Two accessions (ac), IRGC 81825 and CR 100428, both originating from India were resistant to all the six pathotypes and were used for studying the inheritance of bacterial blight resistance and its transfer to cultivated rice *Oryza sativa* cv PR 141.

The F1 of the cross PR 141 *Oryza nivara* acc. 8125 showed a resistant reaction whereas F1 of the cross PR 141 *Oryza nivara* acc. 100428 showed susceptible reaction indicating that the resistance in acc. 8125 was dominant and that of acc. 100428 was recessive.

Table 2. Commercially released MAS rice cultivars in Asia.

Variety/Genotype	Gene combination	Country	Release year/reference
Angke	Xa4 and xa5	Indonesia	2002. Sattari <i>et al.</i> , (2014)
Conde	Xa4 and Xa7	Indonesia	2002
NSIC Rc154 (Tubigan 11)	Xa4 and Xa21	Philippines	2006
Guodao 1	Xa4 and Xa21	China	2004
Improved Pusa Basmati-1	xa5, xa13 and Xa21		2007
PR106	xa5, xa13 and Xa21	India	Singh <i>et al.</i> , (2001)
Samba Mahsuri	xa5, xa13 and Xa21	India	Raman <i>et al.</i> , (2008)
Type 3 Basmati	Xa21, xa13, sd-1	India	Rajpurohit <i>et al.</i> , (2011)
RD6	xa5/Blast R	Thailand	Pinta <i>et al.</i> , (2013)
Mahsuri	Xa4, xa5, xa13 & Xa21	India	Guvvala <i>et al.</i> , (2013)
Hybrids			
Zhongyou 6	Xa21	China	Cao <i>et al.</i> , (2003)
Zhongyou 1176	Xa21	China	Cao <i>et al.</i> , (2003)

Vikal *et al.*, (2007) studied the response of a set of 327 accessions of 13 wild *Oryza* species and cultivated African rice, *Oryza glaberrima*, to infection with seven pathotypes of *Xoo* over a period of 3-4 years. Of these, 67 were resistant or moderately resistant to all pathotypes. These comprised 13 accessions of *Oryza glaberrima*, 5 of *Oryza barthii*, 10 of *Oryza rufipogon*, 4 of *Oryza longistaminata*, 22 of *Oryza nivara*, 6 of *Oryza officinalis*, 2 of *Oryza rhizomatis* and 5 of *Oryza minuta*. Inheritance studies, molecular mapping and transfer of some of these genes into *Oryza sativa* ssp. *indica* are in progress.

Noor *et al.*, (2006) conducted a survey to evaluate responses of three different Basmati rice cultivars against 8 different exotic strains of *Xoo* collected from International Rice Research Institute (IRRI) Manila. In this study, 28-30 days, 48-60 days and 80-90 days old rice plants were inoculated with 8 different strains of *Xoo*, and concluded that there was a direct relationship between the resistance and the age of host plant.

Plant age greatly influenced the varieties that were susceptible at seedling stage and these varieties showed more pronounced resistant response in the later stages. The reaction of a bacterial strain was variable to different rice varieties, the reaction of different bacterial strains was also found variable against the same rice varieties. Ali *et al.*, (2009) evaluated the Screening of Pakistani 15 genotypes revealed Kashmir Basmati as a highly resistant genotype and showed $\geq 75\%$ resistance to all the tested strains/isolates, only YR6W14D3 infect the genotype but the severity was not divesting.

Shah *et al.*, (2009) conducted an experiment comprising 14 species of wild rice and three widely used cultivated varieties of rice in Pakistan. Adult plants were inoculated with virulent isolates of *Xoo* prevailing in NWFP, Pakistan i.e., Xo-103, Xo- 107, Xo-139, Xo-143, Xo-304, Xo-351 and MNR-4. Of all the wild relatives of rice, *Oryza nivara*, *Oryza longistaminata* and *Oryza grandiglumis* showed resistance to all isolates. *Oryza nivara* even did not show any lesion against any isolate.

Remaining wild species showed differential response to the isolates used in the study. These species were resistant to one or few isolates but expressed susceptibility to others. Basmati-385, IR-6 and KSK-282, the cultivated varieties of Pakistan used in study were found susceptible to most of the isolates.

Bacterial blight in Pakistan

In Pakistan bacterial blight disease of rice was recorded for the first time by Mew and Majid, (1977). Ahmad and Majid (1980) observed it on rice varieties IR 6, Palman, Basmati-198 at Rice Research Institute, Kala Shah Kaku and in farmer's field. During rice travelling seminar in 1985 its incidence on farmers field was recorded as 10-15, 15-20, 20-25% in Sindh, Punjab and NWFP respectively (Akhtar and Akram, 1987). Nineteen rice cultivars under NURYT trial in 1985 were tested at 10 locations and its occurrence was noted in almost all provinces of Pakistan (Akhtar and Akram, 1987). Khan *et al.*, (2000) narrated that BB incidence is increasing in Pakistan in recent years especially in Kallar belt that is famous for producing high quality aromatic rice. Akhtar *et al.*, (2003) conducted a survey during the crop year 2002 for monitoring bacterial blight incidence and severity in Punjab, Sindh, Baluchistan, NWFP and Azad Jammu and Kashmir rice growing areas and to study the latest situation of this menace. They reported that Bacterial blight created a serious problem in rice during the crop year 2002. They concluded that bacterial blight incidence and severity in Punjab remained high during Sept-October due to conducive environment (sudden strong wind and rain) at the time of panicle initiation and flowering of rice cultivars.

Resistance characterization of rice cultivars in response to bacterial blight

Bacterial Blight has the potential to become a destructive disease of rice in Pakistan. Generally, the use of resistant cultivars is the most effective method for controlling plant diseases. However, the available rice germplasm in the country is susceptible to virulent isolates of bacterial blight (Akhtar *et al.*, 2003).

Cultivation of resistant varieties is an effective way to protect the crop against bacterial leaf blight (Waheed *et al.*, 2009). Cultural control methods are important, but the primary and most effective means of control is through planting resistant cultivars.

Vera Cruz *et al.*, (1996) observed in their study that different races of the same pathogen exist in the same field on the same cultivar. *Xoo* populations collected from different districts of Indian Punjab found high level of diversity in pathogen population. They also found that BB resistance gene *xa8* and *Xa21* are effective against the prevalent isolates in Indian Punjab followed by *xa5* and *Xa7*. The Basmati rice growing areas of Punjab in Pakistan is adjacent to Indian Punjab; it could be possible that the same genes effects will be seen in Pakistani rice growing areas. However, studies on pathogen populations between countries and within countries have indicated that regionally defined pathogen populations are distinct, which could be attributed to the slow movement/dispersal of the pathogen or slow partitioning of host genotypes (Adhikari *et al.*, 1995).

Development of near isogenic lines

To facilitate characterization of resistant genes and *Xoo* isolates, International Rice Research Institute (IRRI) developed a set of near isogenic lines (NIL) in 1980. Each NIL contained a single *Xa* gene in the background of the susceptible cultivar IR24 (Ogawa *et al.*, 1988). Using these isolines, six BB resistant genes have been cloned (*Xa1*, Yoshimura *et al.*, 1998; *xa5*, Iyer and McCouch, 2004; *xa13*, Chu *et al.*, 2006; *Xa21*, Song *et al.*, 1995; *Xa26*, Sun *et al.*, 2004 and *Xa27*, Gu *et al.*, 2004). The *xa5* allele provides race specific resistance to *Xoo*. Based on candidate gene analysis, *xa5* appears to be unique among resistant genes because it does not fall into any of the predicted resistant gene classes (Blair *et al.*, 2003). Map-based cloning revealed that *xa5* encoded the small subunit of transcription factor IIA (TFIIA γ) (Iyer and McCouch, 2004). A 2-nucleotide substitution at position 39 in the second exon of the gene resulted in an amino acid change from valine (V39) in susceptible cultivars to glutamic acid in resistant.

All resistant cultivars contained glutamic acid at position 39 and all susceptible cultivars contained valine, and some had an additional silent substitution (Iyer and McCouch, 2004). There was no differential expression of either the *xa5* or *Xa5* allele in response to infection. Transformation of the dominant susceptible allele from IR24, an *indica*, into a resistant background resulted in diseased plants, as measured by lesion length and bacterial population growth (Jiang *et al.*, 2006). *Xa3*, *xa5*, and *xa8* appear to convey a wide spectrum of resistance to Asian isolates of the BB pathogen (Ogawa *et al.*, 1988).

Marker assisted selection for resistance to BB in rice

Joseph *et al.*, (2004) undertook study with the objective of combining the important Basmati quality traits with resistance to bacterial blight by a combination of phenotypic and molecular marker assisted selection (MAS). Screening of 13 NIL of rice against four isolates of pathogen from Basmati growing regions identified the *Xa4*, *Xa8*, *xa13* and *Xa21* genes as effective against all the isolates tested. Two or more of these genes in combination imparted enhanced resistance as expressed by reduced average lesion length in comparison to individual genes. The two-gene pyramid line IRBB55 carrying *xa13* and *Xa21* was found equally effective as three/four gene pyramid lines. The two bacterial blight resistance genes present in IRBB55 were combined with Basmati quality traits of Pusa Basmati-1 (PB-I), the most popular high yielding Basmati rice variety used as a recurrent parent (See Table 2 for details).

Incorporation of BB resistance genes into rice cultivars

Major genes or qualitative genes confer a high level of resistance but sometime resistance breaks down due to evolution of new races of the pathogen. At the International Rice Research Institute (IRRI), the resistance gene *Xa4* has been incorporated into most elite lines and cultivars (Ogawa *et al.*, 1988). This gene has provided excellent resistance in East and Southeast Asia.

Elite breeding lines with *xa5* and *Xa7* have also been developed. A gene (*Xa21*) from *Oryza longistaminata* conferring broad spectrum resistance against Asian isolates has been transferred to improved breeding lines. Use of major gene resistance and avoidance of highly susceptible parents have proven effective in obtaining durably resistant cultivars.

Yan *et al.*, (2004) introduced novel bacterial blight resistance gene(s) into a cultivar (cv) of japonica rice *Oryza sativa* (cv. 8411) via somatic hybridization using the wild rice *Oryza meyeriana* as the donor of the resistance gene(s).

Twenty-nine progenies of somatically hybridized plants were obtained. Seven somatically hybridized plants and their parents were used for AFLP (amplified fragment length polymorphism) analysis using 8 primer pairs. Results confirmed that these plants were somatic hybrids containing the characteristic bands of both parents. The morphology of the regenerated rice showed characteristics of both *Oryza sativa* and *Oryza meyeriana*. Two somatic hybrids showed highest resistance and the other eight plants showed moderate resistance.

Conclusions

Bacterial blight is becoming a serious threat to productivity of rice throughout the world. As effective chemical control is not available, therefore, genetic host resistance is the only way to control this manse of rice. Wild species of rice offer a great reservoir of genes and these genes can be effectively transfer to cultivated varieties of rice through wide hybridization and using the methods of genetic engineering. BB is characterized by a high degree of race–cultivar specificity. Therefore, screening for resistance to pathogen populations specific to particular geographical locations and tailoring regional breeding programs accordingly are recommended. Although major genes or qualitative genes confer a high level of resistance but sometime resistance breaks down due to evolution of new races of the pathogen.

Therefore, pyramiding of major resistance genes through marker-assisted selection would be useful to attain durable and broad spectrum resistance.

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