Distribution of Xanthomonas oryzae pv. oryzae DNA Modification Systems in Asia†

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The presence or absence of two DNA modification systems, XorI and XorII, in 195 strains of Xanthomonas oryzae pv. oryzae collected from different major rice-growing countries of Asia was assessed. All four possible phenotypes (XorI⁺ XorII⁺, XorI⁺ XorII⁻, XorI⁻ XorII⁺ and XorI⁻ XorII⁻) were detected in the population at a ratio of approximately 1:2:2:2. The XorI⁺ XorII⁺ and XorI⁻ XorII⁻ phenotypes were observed predominantly in strains from southeast Asia (Philippines, Malaysia, and Indonesia), whereas strains with the phenotypes XorI⁻ XorII⁺ and XorI⁺ XorII⁻ were distributed in south Asia (India and Nepal) and northeast Asia (China, Korea, and Japan), respectively. Based on the prevalence and geographic distribution of the XorI and XorII systems, we suggest that the XorI modification system originated in northeast Asia and was later introduced to southeast Asia, while the XorII system originated in southeast Asia and moved to northeast Asia and south Asia. Genomic DNA from all tested strains of X. oryzae pv. oryzae that were resistant to digestion by endonuclease XorI or its isoschizomer PvuI also hybridized with a 7.0-kb clone that contained the XorII modification system, whereas strains that were digested by XorII or PvuI lacked DNA that hybridized with the clone. Size polymorphisms were observed in fragments that hybridized with the 7.0-kb clone. However, a single hybridization pattern generally was found in XorI⁺ strains within a country, indicating clonal maintenance of the XorII methyltransferase gene locus. The locus was monomorphic for X. oryzae pv. oryzae strains from the Philippines and all strains from Indonesia and Korea.

Xanthomonas oryzae pv. oryzae causes bacterial blight, the most important bacterial disease of rice in Asia (15, 16). Compared to the long history of rice cultivation, the deployment of genes for resistance to X. oryzae pv. oryzae in commercial rice cultivars is relatively recent. The introduction of these genes for resistance into rice is correlated with a change in the pathogenic diversity of X. oryzae pv. oryzae populations, that is, new races of the pathogen emerge and overcome deployed resistance (15, 17). These observations have stimulated much curiosity concerning the contribution of host genotype and other factors to the genetic diversity of the pathogen.

Multilocus molecular markers have been used in conjunction with virulence typing to evaluate the diversity and structure of X. oryzae pv. oryzae populations within and between countries in Asia (1, 3, 6, 11, 12, 21, 27). In general, regionally defined pathogen populations in Asia were found to be distinct (1). This finding could be due either to slow pathogen migration or dispersal or to spatial partitioning of host genotypes (different cultivar preferences between regions). Although populations within a region generally were similar, in some cases genetically similar strains were detected in different regions, suggesting the migration of strains between countries, possibly as a consequence of germ plasm exchange (1, 6). Within one country, the Philippines, significant differentiation in populations was observed between different agroecosystems; that is, populations of X. oryzae pv. oryzae in the cool, mountainous highlands, where one crop of traditional varieties per year is grown, were different from those in the tropical lowlands, where two or three crops of semidwarf, early-maturing rice varieties per year are grown (3). Since several ecological factors in addition to host genotype likely influenced the genetic diversity of the pathogen population collected in that study (3), the magnitude of the contribution of any one of those factors to pathogen diversity is not clear.

To more critically evaluate the genetic structure and movement of X. oryzae pv. oryzae populations throughout Asia and to understand some of the factors that influence the population structure of this pathogen, we have been investigating two X. oryzae pv. oryzae DNA restriction modification (R-M) systems (XorI and XorII) previously shown to be present in the pathogen (5, 28). R-M systems are particularly interesting for such studies, because they are thought to protect the bacterial genome from invasion by introduced bacteriophage or plasmid DNA (9) and thus may inhibit genomic variability due to DNA exchange on uptake. We cloned and sequenced two genes that are part of the XorII R-M system (xorII and xorII-vsr) (5). Not all X. oryzae pv. oryzae strains contained the XorI and XorII modification systems (5, 24), indicating that the systems might prove useful for developing an understanding of the origins of X. oryzae pv. oryzae genetic lineages and their distribution patterns. In this study, we determined the distribution of the two modification systems in a group of X. oryzae pv. oryzae strains collected from throughout Asia. Based on this information, we formulated a hypothesis on the geographic origin and historical migration of the DNA modification systems. In addition, we discuss the potential influence of these modification systems on the genetic stability of X. oryzaepv. oryzae populations.
TABLE 1. Distribution of XorI and XorII DNA modification systems of X. oryzae pv. oryzae in Asiation

<table>
<thead>
<tr>
<th>Region of Asia and country of origin</th>
<th>No. of strains</th>
<th>No. of strains with the following DNA modification system pattern:</th>
<th>Genetic diversity</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>XorI+ XorII</td>
<td>XorI+ XorII</td>
</tr>
<tr>
<td>South</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>India</td>
<td>10</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Nepal</td>
<td>33</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Southeast</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Philippines</td>
<td>64</td>
<td>18</td>
<td>0</td>
</tr>
<tr>
<td>Malaysia</td>
<td>7</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>Indonesia</td>
<td>14</td>
<td>4</td>
<td>0</td>
</tr>
<tr>
<td>Northeast</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>China</td>
<td>43</td>
<td>2</td>
<td>38</td>
</tr>
<tr>
<td>Korea</td>
<td>18</td>
<td>4</td>
<td>14</td>
</tr>
</tbody>
</table>

Genetic diversity in each DNA modification system group

a The distribution of the four different R-M systems was not random within the three geographic regions of Asia (south, southeast, and northeast), based on an analysis by Fisher’s exact test (P = 0.00001).

b The DNA modification system phenotype was determined by sensitivity or resistance to PstI (isoschizomer of XorI) and XorII and/or its isoschizomer PvuII as well as hybridization with xorIM and xorII-vsr genes in pE7.0. Resistance to digestion indicates that the DNA modification system is present (+), and sensitivity to digestion indicates that the system is absent (−).

c Genetic diversity was calculated with the formula \( \left[ n \left( n - 1 \right) \right] / \left( \sum x_i^2 \right) \), where \( x_i \) is the proportion of the i-th RFLP type within a group and \( n \) is the number of strains tested in each group. Data are from RFLP analysis performed with two probes, pEL101 and pBSavrXa10 (1). Diversity was calculated from the combined data for each country. Data for Japan are not reported because RFLP data were not available for these strains.

d Genetic diversity determined with RFLP data as described in footnote c but partitioned for DNA modification system group.

MATERIALS AND METHODS

Bacterial strains, plasmids, and culture media. The 195 strains of X. oryzae pv. oryzae used in this study were obtained from Korea (18 strains collected from five provinces between 1987 and 1989), the Philippines (64 strains collected from a wide range of ecosystems on three different islands, Luzon, Mindanao, and Visayas [see reference 11] between 1972 and 1990), India (10 strains from five states, collected in 1987, 1990, and 1991), Malaysia (7 strains from three provinces, collected between 1962 and 1989), Indonesia (14 strains from two islands, collected in 1976, 1990, and 1992), and Nepal (33 strains from 15 districts, collected between 1987 and 1989) and were provided by K. S. Jin (National Institute of Agricultural Sciences and Technology, Rural Development Administration, Suweon, Korea), T. W. Mew (International Rice Research Institute, Los Baños, the Philippines), S. Gnanumanniam (University of Madras, Madras, India), K. S. Lum (Malaysian Agriculture Research and Development Institute, Serdang, Selangor, Malaysia), R. H. Martini (Bogor Research Institute of Food Crops, Bogor, Indonesia), and T. Adhikari (Institute of Agriculture and Animal Science, Kathmandu, Nepal), respectively. DNAs of strains from China (43 strains from 15 provinces, collected from 1981 to 1992) and Japan (6 strains from five prefectures, collected in 1968, 1971, and 1985) were provided by Q. Zhang (Institute of Crop Breeding and Cultivation, Chinese Academy of Agricultural Science, Beijing, China) and M. Watabe (Sekisui Chemical Co., Ltd., Osaka, Japan), respectively. A summary of data relevant to this communication is included in Table 1; data for each strain, including the site of collection within a country, the year of collection, the race (pathotype), and the restriction fragment length polymorphism (RFLP) type for multilocus probes, are available by request from J. E. Leach.

X. oryzae pv. oryzae strains were cultured in peptone-sucrose broth (26) or nutrient broth (Difco Laboratories, Detroit, Mich.) at 28°C with shaking at 200 rpm. Bacterial genomic DNA was isolated by a lysosyme-sodium dodecyl sulfate lysis procedure (22) modified as described previously (10).

Strains of X. oryzae pv. oryzae (159.14m from China and BLS335 from the Philippines) and strains from various pathovars of X. campestris (pathovars vesicatoria [65-2], alfalfa [KX-1], malvacearum [28], holecica [123], psi [NCPBP762], pruni [ATCC 19316], cucurbitae [NZ2299], fragariae [ICP-BXF122], and phleipratensis [PPDCCS754]) were from L. Claflin, Kansas State University.

Plasmid pE7.0 contains a 7.0-kb fragment from X. oryzae pv. oryzae which includes the gene encoding XorII methyltransferase (xorIM) and a vsr-like gene (very-short-patch-repair endonuclease gene; xorII-vsr) in the vector pBluescript KS+ (Fig. 1) (5). Plasmid pEV2.0 contains xorIM and the 3′ end of xorII-vsr in a 2.0-kb insert, whereas plasmid pEV5.0 contains the 5′ portion of xorII-vsr and 5′-flanking regions in a 5.0-kb fragment. These plasmids were used as probes for hybridization of X. oryzae pv. oryzae genomic DNA that had been digested with EcoRV, EcoRI, and BamHI (see below). Plasmid DNA from Escherichia coli was prepared by the alkaline lysis method as described by Morelle (18).

DNA analysis. The presence of XorI and XorII modification systems in X. oryzae pv. oryzae was determined by the resistance of genomic DNA to digestion with PstI (isoschizomer of XorI) and XorII and/or its isoschizomer PvuII, respectively. Digestion conditions were as described by the enzyme manufacturer (Promega), except that a severalfold excess of each enzyme was added and the mixtures were incubated for 3 h.

RFLP analysis. To analyze the genome organization around the xorIM and xorII-vsr loci, genomic DNA was digested to completion with EcoRI, BamHI, or EcoRV, fractionated by gel electrophoresis, and transferred to nylon membranes (Magna NT; MSI, Westboro, Mass.) as described previously (4). The blot was probed with pE7.0 (Fig. 1). For diversity analysis, RFLP analysis of genomic DNA was performed with two multilocus markers as described previously (1). The probes were plasmids containing a mobile, repetitive DNA element, IS1112 (in plasmid pEL101; 10), and a member of a multicopy avirulence gene family, avrXa10 (in plasmid pBSavrXa10; 7). Genomic DNA of each bacterial strain was digested to completion with BamHI (for hybridization with pBSavrXa10) or EcoRI (for hybridization with pEL101). A 4-bp ladder (Bethesda Research Laboratories) was included in gels as a size standard. The plasmids were labeled with [32P]dCTP by use of a nick translation kit (Bethesda Research Laboratories); vector (pBluescript II and pUC18) DNAs did not hybridize with X. oryzae pv. oryzae genomic DNA (data not shown). High-stringency hybridization, washing conditions, and autoradiography were as described previously (10).

Data analysis. Genetic diversity determined by RFLP analysis with multilocus markers for X. oryzae pv. oryzae subpopulations with the four possible DNA modification system phenotypes was estimated with Nei and Tajima’s haplotypic diversity index (19, 20). The genetic diversity within each R-M group was esti...
RESULTS

DNA modification systems in *X. oryzae* pv. oryzae and their distribution in Asia. Genomic DNAs from a collection of 195 strains of *X. oryzae* pv. oryzae were evaluated for the presence or absence of the *Xor* and *xorII* modification systems (summarized in Table 1). The presence of the *Xor* modification system was assumed if genomic DNA was resistant to digestion with *PstI*, an isoschizomer of *Xor*. The *xorII* modification system was identified by resistance of DNA to digestion with *xorII* or *PvuII* (isoschizomer of *xorII*) and by hybridization of the genomic DNA to clone pE7.0, which contains the *xorII* R-M system (5). DNA from all strains that were resistant to digestion with *Xor* and *PvuII* hybridized with pE7.0, whereas DNA from strains that were digested with the two enzymes did not hybridize with pE7.0.

As determined by Fisher's exact test, the distribution of the *Xor* and *xorII* modification systems in Asia is not random and is differentiated by geographic region (Table 1). Of the four possible phenotypes (*Xor* and *xorII*, *xorI* and *xorII*, *Xor* and *xorII*, and *Xor* and *xorII*), only the *Xor* *xorII* phenotype was found in the 10 strains from the northern, central, and eastern parts of India (Table 1). Most Nepalese strains (27 of 33), also collected from widely separated geographic regions within the country, exhibited the *Xor* *xorII* phenotype. The *xorI* *xorII*+ and *xorI* *xorII*− phenotypes were predominantly observed in strains from southeast Asia (Philippines, Malaysia, and Indonesia). Both phenotypes were present at different sampling sites in the Philippines, indicating that the two phenotypes were widely distributed within the country. The *Xor* *xorII*− phenotype was found in the Philippines in only one group of strains, race 6, which were detected only at a single site. The strains from northeast Asia (north China, Korea, and Japan) exhibited both the *xorI* *xorII*+ and the *xorI* *xorII*− phenotypes, although the most prevalent phenotype in north China (38 of 43 strains) and Korea (14 of 18 strains) was *xorI* *xorII*+. The DNA modification systems (*Xor* *xorII*+ and *xorI* *xorII*−) of the three strains from south China were different from those of the majority of strains collected in north and northeast China and were more similar to those of strains from southeast (*xorI* − *xorII*+) and south (*xorI* − *xorII*) Asia (Table 1).

Genetic diversity of *X. oryzae* pv. oryzae with different DNA modification systems. The genomic diversity in *X. oryzae* pv. oryzae strains with each of the four DNA modification system phenotypes was assessed with RFLP data obtained from an analysis with two multicopy DNA markers, *avrXa10* and *ISI112* (1). Analysis with these markers resulted in a combined total of 64 potential band positions (1). The RFLP data were partitioned for country of origin and for each of the four DNA modification system phenotypes, and the genetic diversity was calculated. Diversity was high when the data were partitioned by country of origin, ranging from 0.59 for Malaysia to 0.98 for India. Diversity was high in all DNA modification system groups, ranging from 0.74 for *Xor* *xorII*+ to 0.97 for *Xor* *xorII*− (Table 1).

Genomic organization of *X. oryzae* pv. oryzae around the *xorII* modification locus. The genomic organization around the *xorII* modification locus was determined by RFLP analysis with the probes pEV2.0 and pEV5.0, which are subclones of a 7.0-kb region (pE7.0) that contains the locus. A total of 33 *X. oryzae* pv. oryzae strains originating from different countries and whose DNA was resistant to digestion with *Xor* were selected at random. *EcoRV* fragments of DNA from the strains were separated by electrophoresis, blotted to membranes and hybridized with either pEV2.0 or pEV5.0. Note that this blot shows hybridization to both probes. Bands labeled with sizes in kilobases hybridized with pEV2.0; note that bands at approximately 0.1 kb are not visible at this exposure. Bands at approximately 8.5 and 9.0 kb (marked with arrowheads) hybridized with pEV5.0.

![FIG. 2. Composite blot showing RFLPs in DNA from *X. oryzae* pv. oryzae strains from different countries. PXO, strains from the Philippines; ID, strains from Indonesia; NXO, strains from Nepal. Strain GD1358 is from China, and strains JW89011 and KA89031 are from Korea. Fragments of genomic DNA generated by digestion with *EcoRV* were separated by electrophoresis, transferred to nylon membranes, and hybridized with either pEV2.0 or pEV5.0. Note that this blot shows hybridization to both probes. Bands labeled with sizes in kilobases hybridized with pEV2.0; note that bands at approximately 0.1 kb are not visible at this exposure. Bands at approximately 8.5 and 9.0 kb (marked with arrowheads) hybridized with pEV5.0.](http://aem.asm.org/lookup/doi/10.1128/AEM.64.10.1665-1673.1998)
cation locus in 33 X. oryzae pv. oryzae strains collected from different countries. The regions upstream of the xorII-vsr gene were highly conserved (a fragment of approximately 8.5 kb), except in one strain from China (GD1358; RFLP type E), while the regions downstream of xorIIM were more polymorphic, with fragments of approximately 5, 6, 7, or 10 kb (Fig. 3). RFLP pattern A was found in DNA from Korean strain JW89011 (from which the Xor II methyltransferase gene was isolated) and from many strains originating in the Philippines, Indonesia, and Korea (Fig. 3). Strains exhibiting both the Xor I and Xor II modification systems were represented in pattern A. RFLP pattern B was characteristic of one Philippine strain (PXO61; Xor II’ Xor II’’) and all Malaysian strains (Xor I’ Xor II’ and Xor I’’ Xor II’’). RFLP types C and D were found only in the six Nepalese strains with the Xor I’ Xor II’’ phenotype (Fig. 3).

Absence of xorII-related DNA in other xanthomonads. The presence or absence of DNA sequences related to the Xor II R-M system in other Xanthomonas species was determined by high-stringency DNA hybridization analysis with pE7.0 as a probe. DNA from strains of X. oryzae pv. oryzae from the Philippines and China did not hybridize with pE7.0. DNA from strains of various X. campestris pathovars (vesicatoria, alfalfa, malvacearum, holocica, pisi, pruni, cucurbitae, fragariae, and phleipratensis), which are pathogenic in a wide variety of hosts, also did not hybridize with pE7.0.

**DISCUSSION**

Based on the nonrandom geographic distribution of XorI and XorII modification systems in X. oryzae pv. oryzae strains, the regions of origin of the modification systems were inferred. The similarity in genome organizations around the xorIIM and xorII-vsr genes indicated that the XorII R-M loci that are widely distributed in Asia are from a common ancestor. The XorII system is present in most strains from southeast Asia (88% contain DNA that is not digested with XorII or PvuI and that does not hybridize with the XorII modification system genes). Therefore, we suggest that the XorII system originated in southeast Asia (the Philippines, Indonesia, and Malaysia) and was distributed from there to south Nepal and northeast Asia (China, Korea, and Japan) (Fig. 4). Although more widely distributed, the XorI system likely originated in northeast Asia (DNA from 95% of the total strains from China and Korea is not digested by XorI or PstI) and moved from there to southeast Asia. Strains containing these systems may have moved between parts of Asia by weather systems, such as typhoons, or on seed during the movement of rice germ plasm (Fig. 4). The lack of either...
The Xor methyltransferase has 10 conserved polypeptide domains that are commonly found in the 5-methylcytosine methyltransferase family among a wide variety of prokaryotes (5, 23). Likewise, the amino acid sequence of the produce of xorII-vsr shows similarity to the deduced amino acid sequences of other vsr homologs that are associated with m5cytosine methyltransferase systems (5, 8, 25). Based on these facts, it is possible that the XorII R-M loci originated from a common ancestor and were transmitted to X. oryzae pv. oryzae through horizontal gene transfer (2). However, the XorII modification genes from X. oryzae pv. oryzae did not hybridize with DNAs from two different X. oryzae pv. oryzae bacteriophage strains (data not shown) or genomic DNAs from several different xanthomonads, including the closely related pathogen X. oryzae pv. oryzicola. Although only a limited number of xanthomonads were tested and although they were tested for hybridization under high-stringency conditions, the findings suggest that the XorII R-M system did not arise recently from other xanthomonads. It is possible that the XorII system evolved after the xanthomonads were differentiated into species and pathovars or that it originated from other prokaryotes.

The genome organization around the region containing genes coding for the XorII R-M system of one Philippine race 1 strain, PXO61, was identical to that of this region in all of the Malaysian strains. This finding suggests either that PXO61 originated from Malaysia or that the Malaysian strains were derived from an introduction of the PXO61 type. Interpretation of these results is complicated by the fact that in a previous study, PXO61 was clustered with other Philippine strains by multicyclic marker-mediated lineage analysis, and this cluster was distant from the cluster containing the Malaysian strains (1). Perhaps the high degree of variability associated with multicopy markers masks differences in genome organization within the modification system. If so, a comparison of multicopy versus single-copy markers might be important for phylogenetic studies of these bacteria (13, 14, 21).

Analysis of the two modification systems in X. oryzae pv. oryzae provided additional insight into the geographic distribution of these systems in this pathogen throughout major rice-growing countries in Asia. After the distribution of a modification system, the particular modification lineages or clones apparently became fixed in the population and maintained their identity. All four phenotypes (XorI*, XorII*, XorI*, XorII*) were found in Asia, and in some cases, mixed populations (more than one phenotype in a region or country) were observed. These mixed populations may have been derived from the introduction of new strains with different modification systems either by humans or by weather systems. This idea suggests that populations of X. oryzae pv. oryzae in different countries share common genetic backgrounds from which loci related to fitness were further selected in a defined ecosystem. For example, the Korean strains with the XorII R-M system might have a genetic background similar to that of the Philippine strains besides race 6,
and the Philippine race 6 strains might be similar to the Indian
and XorI–XorII Nepalese strains.

The genetic diversity of X. oryzae pv. oryzae populations
detected by multicopy markers such as IS112 (10, 29) or
avrXa10 (7) in general was high throughout Asia, in spite of
the presence or absence of different DNA modification systems.
This finding suggests that the R-M systems may not play a role
in reducing the genetic diversity of populations. However,
the markers used in these studies to measure diversity were either
themselves mutagenic (the mobile IS112 element) or prone to
selection (the avirulence gene family). Thus, these multicopy
markers may produce an inflated measurement of diversity.
Analysis of diversity with less variable components of the ge-
nome may provide more information on the effect of R-M
systems on the genetic diversity of these bacteria.

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