MPMI Vol. 37, No. 12, 2024, pp. 814–818, https://doi.org/10.1094/MPMI-05-24-0062-SC

SHORT COMMUNICATION

Evolutionary and Epidemiological Insights from Historical and Modern Genomes of *Xanthomonas oryzae* pv. *oryzicola*, the Causal Agent of Bacterial Leaf Streak of Rice

Mathilde Hutin,[1,†] Sara Carpenter,[2] Shivrajani Baruah,[2] Paola Campos,[3] Karine Boyer,[3] Dodelys Andriantsimialona,[4] Solo Hery Rapanarivo,[4] Olivier Pruvost,[3] Nathalie Becker,[3,5] Lionel Gagnevin,[1] Ralf Koebnik,[1] Boris Szurek,[1] Ousmane Koita,[6] Adam J. Bogdanove,[2] and Adrien Rieux[3,†]

[1] Plant Health Institute of Montpellier, Institut Agro, University of Montpellier, IRD, CIRAD, INRAE, Montpellier, France
[2] Plant Pathology and Plant-Microbe Biology Section, School of Integrative Plant Science, Cornell University, Ithaca, NY 14853, U.S.A.
[3] CIRAD, UMR PVBMT, Saint Pierre F-97410, La Réunion, France
[4] TAN Herbarium, Parc Botanique et Zoologique de Tsimbazaza (PBZT), Département FLORE, Antananarivo, Madagascar
[5] Muséum national d'histoire naturelle, UMR ISYEB (Institut de Systématique Évolution Biodiversité), MNHN, CNRS, Sorbonne Université, EPHE, Université des Antilles, 75005, Paris, France
[6] Laboratoire de Biologie Moléculaire Appliquée, Université des Sciences, des Techniques et des Technologies de Bamako, Faculté des Sciences et Techniques, BP E 3206, Bamako, Mali

Accepted for publication 10 September 2024.

***Xanthomonas oryzae* pv. *oryzicola* (*Xoc*) causes bacterial leaf streak (BLS) of rice. This disease represents a major constraint for rice production, which is a crop feeding more than half of the world's population. *Xoc* was first described in 1918 in the Philippines and is prevalent in southeast Asia. Today, BLS is also omnipresent in both East- and West-Africa, where the disease was first reported in the early 1980s. The appearance of *Xoc* in Africa decades after its first report in Asia suggests that the disease could have been introduced from Asia to Africa. Strict conservation of five transcription activator-like (TAL) effectors in whole-genome sequences of 10 strains of *Xoc* including three from West-Africa and seven from Asia also support this hypothesis. East-Africa, especially Madagascar, where the disease was first described in 1985 is located at the interface between Asia and Africa, hence representing an interesting region to explore the link between strains from Asia and West-Africa. In this study, we did the following: (i) reconstructed the genome of a historical *Xoc* strain from a herbarium specimen of rice showing symptoms of BLS that was sampled in Madagascar in 1931, 50 years before the first description of the disease, and (ii) sequenced nine new modern strains, including five from Madagascar and East-Africa. The analysis of those new genomes along with previously published ones shed light within the evolutionary and epidemiological history of *Xoc*.**

Keywords: ancient genomics, avirulence factors, bacterial dissemination routes, bacterial leaf streak, *Xanthomonas oryzae* pv. *oryzicola* (*Xoc*)

[†]Corresponding authors: A. Rieux; adrien.rieux@cirad.fr, and M. Hutin; mathilde.hutin@ird.fr

Author contributions: All authors participated in scientific discussion of the manuscript and provided comments, critiques, and/or approvals prior to submissions and revisions. A.R., L.G., N.B., O.P., A.J.B., M.H., and B.S. conceptualized the research project. D.A. and S.H.R. provided access to the historical material. P.C., A.R., K.B., and N.B. performed molecular lab work on the historical specimen. S.C., S.B., M.H., R.K., O.K., and A.J.B. produced the contemporary genomes. S.C., S.B., and M.H. performed plant inoculation work. A.R., M.H., S.C., S.B., and N.B. performed all the genetic analyses. A.R. and M.H. wrote the first draft, and all authors contributed to the final version.

Disclaimer: Collection of any plant material used in this study complies with institutional, national, and international guidelines. Permission to collect and analyze historical specimens was provided by the herbarium institutions and their curators.

Funding: Support was provided by the European Regional Development Fund GURDT I2016-1731-0006632, the Agropolis Foundation (E-SPACE 1504-004; MUSEOVIR 1600-004), Genoscope AP 09/10 project number 18, and the Agence Nationale de la Recherche (ANR-17-CE35-0009-01; ANR-2010-BLAN-1723-01).

e-Xtra: Supplementary material is available online.

The author(s) declare no conflict of interest.

Xanthomonas oryzae pv. oryzicola (Xoc) causes bacterial leaf streak (BLS) of rice, which can result in yield losses of up to 30% (Liu et al. 2014). This widely distributed pathogen was first reported in 1918 in the Philippines and other Asian countries (Ou 1985) before being observed in West-Africa and Madagascar in the early 1980s (Buddenhagen 1985; Gonzalez et al. 2007). Since the first observation of BLS in Madagascar, its presence has been molecularly confirmed in several East-African countries including Uganda, Burundi, Kenya, and Tanzania (Afolabi et al. 2014; Onaga et al. 2018; Poulin et al. 2014). Over the past 15 years, it has become a major problem in West-Africa (Diallo et al. 2021; Tall et al. 2022; Wonni et al. 2014). Irrigation, wind, rain, typhoons, and transfer of infected seeds could have favored

the dissemination of the disease at different scales (Niño-Liu et al. 2006).

Xoc enters leaves via stomata or wounds and multiplies in the intercellular spaces of parenchyma cells. BLS is characterized by translucent yellow streaks delineated by the leaf veins from which exudates are formed that promote the dispersion of the bacteria (Niño-Liu et al. 2006). In many *Xanthomonas* species, transcription activator-like effectors (TALE) are major determinants of pathogenicity. Once delivered into host cells via the type III secretion system, these sequence-specific DNA-binding proteins act as eukaryotic transcription factors capable of upregulating targeted plant genes (Boch and Bonas 2010). Some of them act as major virulence factors inducing susceptibility (*S*) genes, which are so-called because their induction is required for full disease development (Hutin et al. 2015). *X. oryzae* is the species with the highest number of TALEs observed so far, ranging from 7 to 28 with the maximum for the pathovar *oryzicola* (Scholze and Boch 2011). Of the average 26 TALEs in *Xoc* strains across the world, only two of them are known to have a role in virulence. The TALE Tal2g, which is conserved in West-African and Asian strains of *Xoc*, induces the only *S* gene known to BLS, *OsSULTR3;6* (Cernadas et al. 2014). The second is the truncated TALE (truncTALE) Tal2h, which is encoded by what was first considered a pseudogene. Tal2h suppresses resistance to BLS mediated by the resistance (*R*) gene *Xo1*, which is found in the American heirloom rice variety Carolina Gold Select (Read et al. 2016; Triplett et al. 2016). Interestingly, truncTALE sequences vary, and in a selection of Asian and West-African *Xoc* strains examined, they were found to be functional only in Asian strains but not in West-African ones (Read et al. 2016). Because East-African strains of *Xoc* have only been isolated more recently, their TALE, truncTALE, and other type III-secreted effector (T3E) content have not been characterized. For the same reason, East-African *Xoc* are not part of the two pioneering investigations of *Xoc* genetic diversity worldwide.

Using a multilocus variable-number tandem-repeat analysis (MLVA16) scheme, Poulin et al. (2015) investigated the genetic relationships of 152 strains of *Xoc* from Asia and West-Africa. They showed that all the African strains group in one cluster and most of the Asian strains group in a second one. Interestingly, two strains from China were closer to West-African strains than Asian ones. In a study mainly focused on TALE repertoire analysis, Wilkins et al. (2015) sequenced by long read technology the full genomes of 10 *Xoc* strains, including three West-African strains. They showed that based on their TALE content, it was possible to distinguish Asian from West-African strains. However, the authors highlighted a strict conservation of five TALEs across the 10 strains. Since no TALEs are conserved between African and Asian strains of *X. oryzae* pv. *oryzae* (*Xoo*), this suggests a different evolutionary pattern for *Xoc* and *Xoo*. The difference could be explained by a more recent introduction of *Xoc* than *Xoo* into Africa or by weaker diversifying selection or greater gene flow influencing *Xoc* in East-Africa. In this context, recently isolated strains from East-Africa especially from Madagascar, at the interface between Asia and West-Africa, are of particular interest to understand the relationship between Asian and West-African strains and to better understand *Xoc* dissemination routes.

To this aim, we sequenced the genomes of five new strains from Madagascar, Mali, and Tanzania using PacBio long-read technology and of four other genomes from strains isolated in East-Africa (Burundi and Uganda) and West-Africa (Burkina Faso) using Illumina short-read technology. Additionally, we sequenced one historical genome from an herbarium specimen sampled in Madagascar using Illumina (Supplementary Table S1; Supplementary Materials).

The ability to sequence microbial genomes from ancient biological material such as herbarium specimens provides a rich source of information to better understand pathogen evolution and disease emergence (Yoshida et al. 2014). First, the association of disease symptoms on an herbarium specimen with information about those specimens (collection date, geographic location, host species, or other phenotypic traits) may allow a direct update of past disease occurrence, distribution, and host range. Second, historical and modern genomes can be compared with detect changes in genetic content and arrangement over time, such as the loss or gain of functional genes or the change of ploidy levels, for both pathogens and their host plants (Martin et al. 2013). Finally, robust phylogenies including both modern and ancient individuals allow how crop bacterial pathogens emerge and their dissemination routes to be deciphered (Duchêne et al. 2020; Vinatzer et al. 2014), as recently illustrated in a study focusing on the bacterial crop pathogen *X. citri* pv. *citri* causing Asiatic citrus canker (Campos et al. 2023).

Historical specimen TAN_200431, an *Oryza sativa* sample from Nanisana, Antananarivo, Madagascar, dated 1931 (Fig. 1) was selected for its BLS-like symptoms. Total DNA was carefully extracted in a bleach-cleaned facility with no prior exposure to modern *Xoc* DNA, was converted into an Illumina library, and was sequenced, generating 130 million paired-end

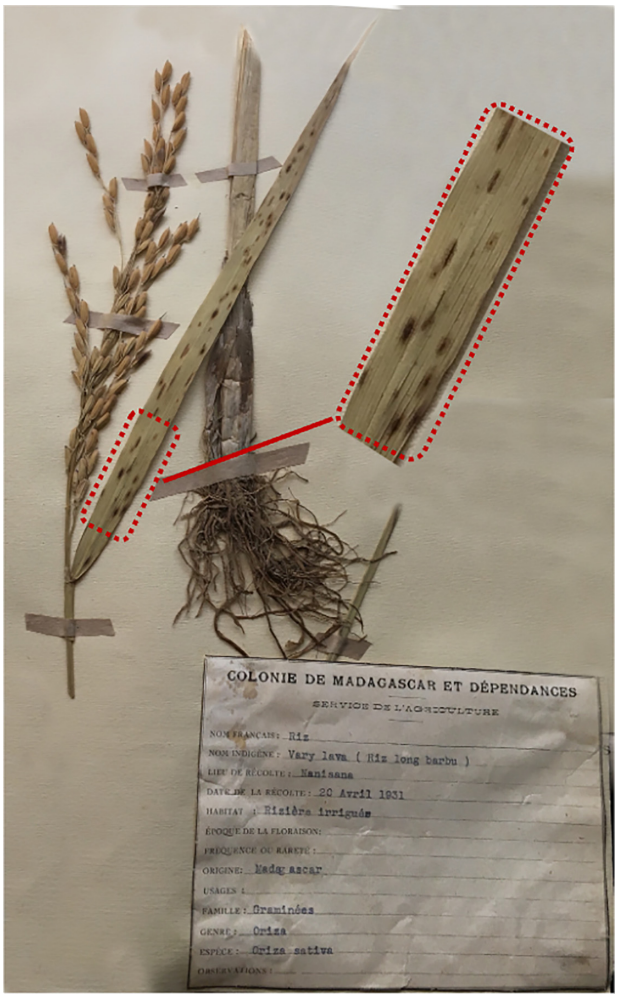

Fig. 1. Rice (*Oryza sativa*) specimen in collection at Tsimbazaza National Madagascar Herbarium (TAN). This rice specimen was collected from Nanisava District, Tananarive, Madagascar, in April 1931 and was deposited in the Tsimbazaza National Madagascar Herbarium. Bacterial leaf streak (BLS)-like symptoms are highlighted with red dotted frames.

reads with a base call accuracy of 99.89 to 99.98%. Approximately 3.90% of the generated reads were assigned to *Xoc* using BLASTn, confirming the presence of the bacterial pathogen within the 1931 historical specimen. Interestingly, our finding constitutes the oldest report of BLS in Madagascar, predating by more than 50 years previous descriptions made in this country (Buddenhagen 1985). We designated the inferred historical isolate as HERB_Xoc_1931. As ancient DNA typically presents cytosine deamination at fragment extremities (Dabney et al. 2013), we analyzed such degradation patterns using the dedicated tool mapDamage2 (Jónsson et al. 2013). The HERB_Xoc_1931 sequences displayed 5′ C > T average substitution rates at terminal nucleotides of 5.2%, decreasing exponentially along the DNA molecule, and authenticated the historical nature of HERB_Xoc_1931. As expected, modern strains displayed no such decay (Fig. 2A). After raw-reads correction for damaged nucleotides and quality checking, the HERB_Xoc_1931 genome was reconstructed by mapping the reads to the reference *Xoc* genome sequence, GenBank accession CP003057 (Philippines strain BLS256). The proportion of the reference genome covered at 1× was 96.9%, and the average number of mapped reads at each base of the reference genome was 35× (Fig. 2B).

To gain insight into *Xoc* population structure, we constructed a phylogeny using the 1931 historical genome and genomes of 20 more modern *Xoc* isolates, collected between 1964 and 2013, in total representing seven West-African strains, five East-African strains, and eight Asian strains (Fig. 3A). Using ClonalFrameML, a total of 22,202 recombination-free single nucleotide polymorphisms (SNPs) were identified. From this SNP alignment, a maximum-likelihood (ML) phylogeny was built with RAxML using the genome of the *Xoo* PX099^{A} strain as an outgroup (Fig. 3C). The global *Xoc* phylogeny divided into two main clusters, with Cluster 1 containing six Asian strains and Cluster 2 comprising the other isolates from various geographical origins. Cluster 2 is subdivided into subclade 2A containing all West-African strains and subclade 2B consisting of East-African strains (including the historical genome) and two Asian strains (from India and China). Subclade 2B genetic structure shows interesting patterns, with the historical genome clustering with a strain from Tanzania rather than with its Malagasy counterpart and the modern Malagasy strains being intermixed with two Asian strains. In addition to the phylogenetic analysis, we computed nucleotide diversity within region (average number of nucleotide differences per site between two genome sequences in all possible pairs of strains in that region) (Fig. 3B). At a regional scale, diversity appeared significantly higher in Asia than in Africa, with East- and West-African *Xoc* strains showing no significant difference. Interestingly, phylogenetic Cluster 1 shows significantly lower values compared with all other groups: East-African strains alone, Cluster 2A (same as West-African strains), Cluster 2B (East-African strains with two Asian phylogenetically related strains), and finally Asian strains (groups sorted in ascending order of respective diversity values). Altogether, the phylogenetic structure and observed genetic diversity suggest independent introductions into East- and West-Africa or divergence after a single introduction, spread, and geographic isolation of *Xoc* in East- and West-Africa. Moreover, *Xoc* may have entered Madagascar at least two times. Finally, the presence of temporal signal (i.e., progressive accumulation of mutations over time) within the *Xoc* phylogenetic tree was tested with Phylostems (Supplementary Materials). By linear regression analysis, no significant linear relationship was detected between root-to-tip distances and sampling ages, at any internal node, impeding the estimation of any divergence time or substitution rate using tip-dating methods (Rieux and Balloux 2016).

Since East-African *Xoc* strains cluster with Asian *Xoc* strains, we investigated whether East-African *Xoc*, like Asian *Xoc*, can suppress *Xo1*-mediated resistance. We also tested their compatibility with the *Xa1* resistance gene, a functional homolog and apparent allele of *Xo1* originally cloned from the rice variety Kogyoku (C. Ji et al. 2020; Z. Ji et al. 2016; Read et al. 2016, 2020; Yoshimura et al. 1998). We syringe-infiltrated leaves of 7-week-old Carolina Gold Select plants (*Xo1*), plants of the variety IR24 (which has no *Xo1* or *Xo1*-like resistance gene), and the IR24 near-isogenic line IRBB1 (which carries *Xa1*) with two Malagasy strains and one Tanzanian strain of *Xoc* (Fig. 4). The West-African strains of *Xoc* MAI3 and Selingue 50 from Mali and the *Xoc* strain BLS256 from the Philippines were included as controls. As expected, Carolina Gold Select and IRBB1 developed water-soaked lesions typical of the disease when infiltrated with the Asian *Xoc* strain BLS256 and triggered a hypersensitive response (HR) indicative of resistance when infiltrated with the West-African *Xoc* strains MAI3 and Selingue 50. Interestingly, the three East-African strains, as their Asian

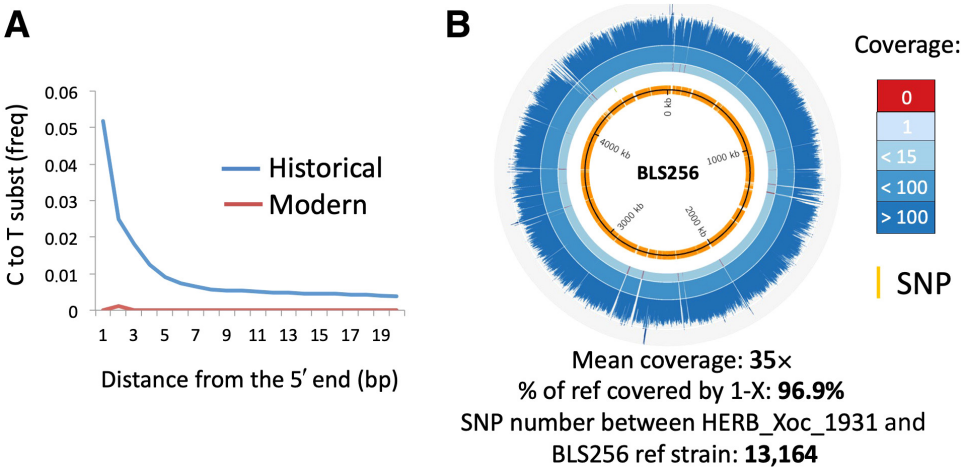

Fig. 2. Authentication and reconstruction of a historical *Xanthomonas oryzae* pv. *oryzicola* genome. **A,** Postmortem DNA damage patterns measured as the frequency of C to T substitutions (subst) from the 5′ end in 1931 historical (blue) and modern (ref BLS256) samples, respectively. **B,** Sequence coverage plot. Blue and red rays indicate regions of the historical genome that are either covered (depth ≥1) or not covered (depth = 0), respectively. The inner circle represents the BLS256 reference genome to which historical reads were aligned. Single nucleotide polymorphisms (SNPs) identified between the historical and the reference genome (n = 13,164) are displayed with orange lines.

counterparts, resulted in water-soaked lesions in Carolina Gold and IRBB1. Consistent with this result, the truncTALEs of these Malagasy and Tanzanian *Xoc* strains display C- and N-terminal regions more similar to those of Asian strains than to West-African strains and, notably, 100% identity to that of the Indian strain BXOR1 (Supplementary Fig. S1). As in the Indian strain, the truncTALEs from the Malagasy strains contain 18 repeats, whereas the one from the Tanzanian strain has 17 (Supplementary Fig. S1). Therefore, we conclude that the East-African strains suppress resistance mediated by *Xo1* and *Xa1* by virtue of the truncTALEs they harbor.

Finally, we investigated the overall T3E content in the HERB_Xoc_1931 assembly by determining the presence or absence of the 27 T3E genes found in BLS256 (Supplementary Table S2) and by examining hits to truncTALE genes (Supplementary Fig. S1). All 27 T3E genes are present. Similarly, both C- and N-terminal regions of TruncTALE were shown to be conserved within the HERB_Xoc_1931 historical genome, with an N-terminal amino acid identity of 98.26% observed with the strain BLS256 (Supplementary Fig. S1). However, neither the repeat regions nor the total numbers of TALE and truncTALE genes could be distinguished due to the short-read sequencing technology used and the fragmentation of the historical DNA.

In summary, in this study, we reconstructed the genome of a historical *Xoc* strain from a BLS-infected herbarium specimen of rice sampled in Madagascar in 1931, 50 years before the first report of BLS in the island. We generated nine additional new genome sequences representing more modern isolates from East- and West-Africa, and we analyzed these along with 11 previously published genome sequences representing strains from Asia and West-Africa. Despite the relatively small number of genomes examined, our study provides new insight into the evolutionary and epidemiological history of *Xoc* and illustrates how historical herbarium specimens can augment that insight. Expanded analysis, including a greater number of modern and historic *Xoc* genomes, will allow for a finer characterization of divergence times and invasive routes, especially in Madagascar and East-Africa.

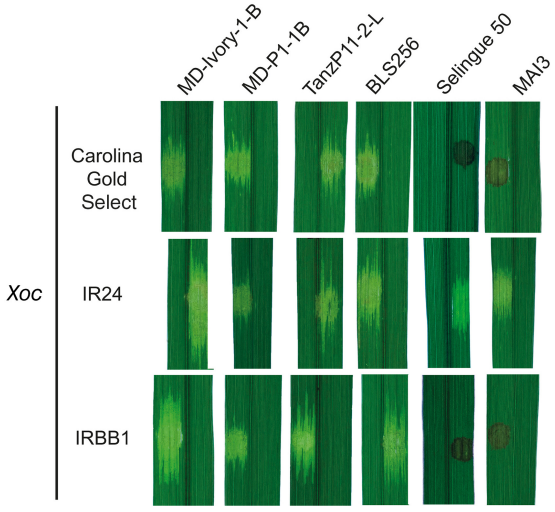

Fig. 4. East-African strains of *Xanthomonas oryzae* pv. *oryzicola* (*Xoc*) like Asian ones are controlled by *Xo1* and *Xa1* genes. Leaves of rice accessions Carolina Gold Select, which carries *Xo1*; IRBB1, which carries *Xa1*; and IR24, which carries neither, were infiltrated with two *Xoc* strains from Madagascar (MD-Ivory-1-B and MD-P1-1B) and a strain from Tanzania (TanzP11-2-L). BLS256, a well-studied strain from the Philippines that expresses the truncTALE Tal2h and therefore overcomes *Xa1* and *Xo1* and two strains from Mali (MAI3 and Selingue 50) that express no functional truncTALE were included for reference. Leaves were photographed at 7 days postinoculation.

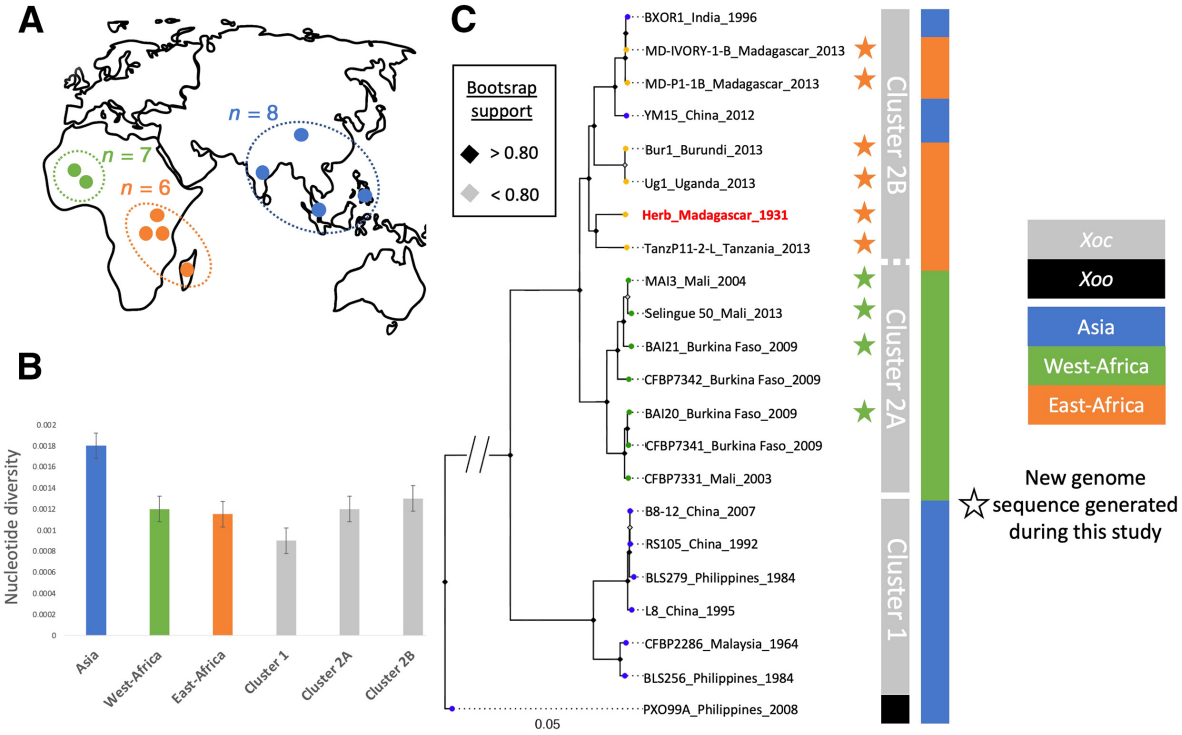

Fig. 3. Geographic distribution and population genomic analysis of *Xanthomonas oryzae* pv. *oryzicola* (*Xoc*) strains examined. **A,** Geographic origin of the 21 *Xoc* strains examined in this study. The number of strains for each region is indicated. **B,** Nucleotide diversity (average number of nucleotide differences per site between two genome sequences across all possible pairs in the region) computed within either each region or genetic cluster. **C,** Maximum-likelihood tree of the 21 *Xoc* strains built from 20,202 nonrecombining single nucleotide polymorphisms (SNPs) using a *Xanthomonas oryzae* pv. *oryzae* (*Xoo*) strain as an outgroup. The 1931 *Xoc* historical genome sequence is highlighted in red. Node support values with bootstrap above 0.8 are indicated by black diamonds. Tips are colored according to geographic origin, as indicated by the map at the top left and the key on the right.

Data Availability

The authors confirm that all data used in this study are fully available without restriction. Raw reads and/or genome assemblies were deposited to the National Center for Biotechnology Information (NCBI) Sequence Read Archive (SRA) and GenBank, respectively, under accession numbers listed in Supplementary Table S1.

Acknowledgments

Computational work was performed on the CIRAD-UMR AGAP HPC data center of the South Green bioinformatics platform (http://www.southgreen.fr/) and MESO@LR-Platform at the University of Montpellier (https://hal.umontpellier.fr/MESO). Laboratory work was conducted on the Plant Protection Platform (3P, IBISA). We are grateful to Pierre Lefeuvre (Cirad, Saint-Pierre, Ile de la Réunion, France) and Lucie Poulin (IRD Montpellier, France) for help with genome assemblies and for technical assistance, respectively.

Literature Cited

Afolabi, O., Milan, B., Amoussa, R., Koebnik, R., Poulin, L., Szurek, B., Habarugira, G., Bigirimana, J., and Silue, D. 2014. First report of *Xanthomonas oryzae* pv. *oryzicola* causing bacterial leaf streak of rice in Burundi. Plant Dis. 98:1426.

Boch, J., and Bonas, U. 2010. *Xanthomonas* AvrBs3 family-type III effectors: Discovery and function. Annu. Rev. Phytopathol. 48:419-436.

Buddenhagen, I. W. 1985. Rice disease evaluation in Madagascar. Int. Rice Commun. Newsl. 34:74-78.

Campos, P. E., Pruvost, O., Boyer, K., Chiroleu, F., Cao, T. T., Gaudeul, M., Baider, C., Utteridge, T. M. A., Becker, N., Rieux, A., and Gagnevin, L. 2023. Herbarium specimen sequencing allows precise dating of *Xanthomonas citri* pv. *citri* diversification history. Nat. Commun. 14:4306.

Cernadas, R. A., Doyle, E. L., Niño-Liu, D. O., Wilkins, K. E., Bancroft, T., Wang, L., Schmidt, C. L., Caldo, R., Yang, B., White, F. F., Nettleton, D., Wise, R. P., and Bogdanove, A. J. 2014. Code-assisted discovery of TAL effector targets in bacterial leaf streak of rice reveals contrast with bacterial blight and a novel susceptibility gene. PLoS Pathog. 10: e1003972.

Dabney, J., Meyer, M., and Pääbo, S. 2013. Ancient DNA damage. Cold Spring Harb. Perspect. Biol. 5:a012567.

Diallo, A., Zougrana, S., Sawadogo, M., Kone, D., Silué, D., Szurek, B., Wonni, I., and Hutin, M. 2021. First report of bacterial leaf streak disease of rice caused by *Xanthomonas oryzae* pv. *oryzicola* in Ivory Coast. Plant Dis. 105:4147.

Duchêne, S., Ho, S. Y. W., Carmichael, A. G., Holmes, E. C., and Poinar, H. 2020. The recovery, interpretation and use of ancient pathogen genomes. Curr. Biol. 30:R1215-R1231.

Gonzalez, C., Szurek, B., Manceau, C., Mathieu, T., Séré, Y., and Verdier, V. 2007. Molecular and pathotypic characterization of new *Xanthomonas oryzae* strains from West Africa. Mol. Plant-Microbe Interact. 20:534-546.

Hutin, M., Pérez-Quintero, A. L., Lopez, C., and Szurek, B. 2015. MorTAL Kombat: The story of defense against TAL effectors through loss-of-susceptibility. Front. Plant Sci. 6:535.

Ji, C., Ji, Z., Liu, B., Cheng, H., Liu, H., Liu, S., Yang, B., and Chen, G. 2020. *Xa1* allelic *R* genes activate rice blight resistance suppressed by interfering TAL effectors. Plant Commun. 1:100087.

Ji, Z., Ji, C., Liu, B., Zou, L., Chen, G., and Yang, B. 2016. Interfering TAL effectors of *Xanthomonas oryzae* neutralize *R*-gene-mediated plant disease resistance. Nat. Commun. 7:13435.

Jónsson, H., Ginolhac, A., Schubert, M., Johnson, P. L. F., and Orlando, L. 2013. mapDamage2.0: Fast approximate Bayesian estimates of ancient DNA damage parameters. Bioinformatics 29:1682-1684.

Liu, W., Liu, J., Triplett, L., Leach, J. E., and Wang, G.-L. 2014. Novel insights into rice innate immunity against bacterial and fungal pathogens. Annu. Rev. Phytopathol. 52:213-241.

Martin, M. D., Cappellini, E., Samaniego, J. A., Zepeda, M. L., Campos, P. F., Seguin-Orlando, A., Wales, N., Orlando, L., Ho, S. Y. W., Dietrich, F. S., Mieczkowski, P. A., Heitman, J., Willerslev, E., Krogh, A., Ristaino, J. B., and Gilbert, M. T. P. 2013. Reconstructing genome evolution in historic samples of the Irish potato famine pathogen. Nat. Commun. 4:2172.

Niño-Liu, D. O., Ronald, P. C., and Bogdanove, A. J. 2006. *Xanthomonas oryzae* pathovars: Model pathogens of a model crop. Mol. Plant Pathol. 7:303-324.

Onaga, G., Murori, R., Habarugira, G., Nyongesa, O., Bigirimana, J., Oliva, R., Vera Cruz, C., Onyango, G., Andaku, J., and Ongom, J. 2018. First report of *Xanthomonas oryzae* pv. *oryzicola* causing bacterial leaf streak of rice in Kenya. Plant Dis. 102:1025.

Ou, S. H. 1985. Rice Diseases. Commonwealth Mycological Institute, Kew, U.K.

Poulin, L., Grygiel, P., Magne, M., Gagnevin, L., Rodriguez-R, L. M., Serna, N. F., Zhao, S., El Rafii, M., Dao, S., Tekete, C., Wonni, I., Koita, O., Pruvost, O., Verdier, V., Vernière, C., and Koebnik, R. 2015. New multilocus variable-number tandem-repeat analysis tool for surveillance and local epidemiology of bacterial leaf blight and bacterial leaf streak of rice caused by *Xanthomonas oryzae*. Appl. Environ. Microbiol. 81: 688-698.

Poulin, L., Raveloson, H., Sester, M., Raboin, L.-M., Silué, D., Koebnik, R., and Szurek, B. 2014. Confirmation of bacterial leaf streak caused by *Xanthomonas oryzae* pv. *oryzicola* on rice in Madagascar. Plant Dis. 98:1423.

Read, A. C., Moscou, M. J., Zimin, A. V., Pertea, G., Meyer, R. S., Purugganan, M. D., Leach, J. E., Triplett, L. R., Salzberg, S. L., and Bogdanove, A. J. 2020. Genome assembly and characterization of a complex zfBED-NLR gene-containing disease resistance locus in Carolina Gold Select rice with Nanopore sequencing. PLoS Genet. 16:e1008571.

Read, A. C., Rinaldi, F. C., Hutin, M., He, Y.-Q., Triplett, L. R., and Bogdanove, A. J. 2016. Suppression of *Xo1*-mediated disease resistance in rice by a truncated, non-DNA-binding TAL effector of *Xanthomonas oryzae*. Front. Plant Sci. 7:1516.

Rieux, A., and Balloux, F. 2016. Inferences from tip-calibrated phylogenies: A review and a practical guide. Mol. Ecol. 25:1911-1924.

Scholze, H., and Boch, J. 2011. TAL effectors are remote controls for gene activation. Curr. Opin. Microbiol. 14:47-53.

Tall, H., Lachaux, M., Diallo, A., Wonni, I., Tékété, C., Verdier, V., Szurek, B., and Hutin, M. 2022. Confirmation report of bacterial leaf streak disease of rice caused by *Xanthomonas oryzae* pv. *oryzicola* in Senegal. Plant Dis. 106:2253.

Triplett, L. R., Cohen, S. P., Heffelfinger, C., Schmidt, C. L., Huerta, A. I., Tekete, C., Verdier, V., Bogdanove, A. J., and Leach, J. E. 2016. A resistance locus in the American heirloom rice variety Carolina Gold Select is triggered by TAL effectors with diverse predicted targets and is effective against African strains of *Xanthomonas oryzae* pv. *oryzicola*. Plant J. 87:472-483.

Vinatzer, B. A., Monteil, C. L., and Clarke, C. R. 2014. Harnessing population genomics to understand how bacterial pathogens emerge, adapt to crop hosts, and disseminate. Annu. Rev. Phytopathol. 52:19-43.

Wilkins, K. E., Booher, N. J., Wang, L., and Bogdanove, A. J. 2015. TAL effectors and activation of predicted host targets distinguish Asian from African strains of the rice pathogen *Xanthomonas oryzae* pv. *oryzicola* while strict conservation suggests universal importance of five TAL effectors. Front. Plant Sci. 6:536.

Wonni, I., Cottyn, B., Detemmerman, L., Dao, S., Ouedraogo, L., Sarra, S., Tekete, C., Poussier, S., Corral, R., Triplett, L., Koita, O., Koebnik, R., Leach, J., Szurek, B., Maes, M., and Verdier, V. 2014. Analysis of *Xanthomonas oryzae* pv. *oryzicola* population in Mali and Burkina Faso reveals a high level of genetic and pathogenic diversity. Phytopathology 104:520-531.

Yoshida, K., Burbano, H. A., Krause, J., Thines, M., Weigel, D., and Kamoun, S. 2014. Mining herbaria for plant pathogen genomes: Back to the future. PLoS Pathog. 10:e1004028.

Yoshimura, S., Yamanouchi, U., Katayose, Y., Toki, S., Wang, Z.-X., Kono, I., Kurata, N., Yano, M., Iwata, N., and Sasaki, T. 1998. Expression of *Xa1*, a bacterial blight-resistance gene in rice, is induced by bacterial inoculation. Proc. Natl. Acad. Sci. U.S.A. 95:1663-1668.