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REVIEW

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The dynamics of *Phytophthora infestans* populations in the major potato-growing regions of Asia – A review

Sanjoy Guha Roy[1] | Tanmoy Dey[1] | David E. L. Cooke[2] | Louise R. Cooke[3]

[1]Department of Botany, West Bengal State University, Kolkata, India

[2]Cell and Molecular Sciences, The James Hutton Institute, Dundee, UK

[3]School of Biological Sciences, Queen's University Belfast, Belfast, UK

Correspondence
Sanjoy Guha Roy, Department of Botany, West Bengal State University, Kolkata 700126, India.
Email: s_guharoy@yahoo.com

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Abstract

Asia is now the largest potato-producing region of the world and late blight, caused by *Phytophthora infestans*, is the most important pathogen limiting production. This review documents, in both the historical and the current context, the population structure of *P. infestans* in the major areas of potato production in Asia. Information from diverse sources regarding the stated or inferred clonal pathogen lineages present, population changes, and possible migration routes of the pathogen into the countries of this region have been reviewed to aid researchers and those involved in managing late blight in Asia. The single most important factor for population change and resultant epidemics in this region has been found to be migration of pathogen genotypes from Europe and the Americas. Reducing the impact of such migration in the future will necessitate putting in place improved phytosanitary measures. To achieve this, data sharing using global networks such as AsiaBlight and EuroBlight is imperative.

KEYWORDS

epidemic, genetic diversity, late blight, migration, *Phytophthora infestans*, population structure

1 | INTRODUCTION

Potatoes are the world's most important non-cereal food crop in terms of global consumption (Devaux et al., 2014), and in Asia, now the centre of world potato production, they are cultivated and consumed across regions with diverse geography and weather. However, despite being the largest continent on the planet, Asia is not easily defined; its boundaries are imaginary and some countries that the United Nations classifies as belonging to Asia (United Nations, Department of Economic & Social Affairs, Statistics Division, 2020) fall partly into other continents. This review focuses on the major potato-producing countries of Asia, which are now estimated to produce c.40% of the world potato tonnage (FAOSTAT, 2020). Transcontinental countries of the Middle East, which also have land in Europe and/or Africa, are not included, nor is Russia, which has land mass both in Europe and Asia.

Potatoes were probably introduced to Asia in the late 16th and early 17th centuries by traders from Europe. Over the last 50 years, potato production has increased dramatically, owing to an increase in both the area where they are grown and, as a consequence of improved agricultural practices, the yield. This has occurred most notably in China and India since the 1960s (Scott & Suarez, 2012). Worldwide, in 2018, China was the largest producer of potatoes, with India the second largest (FAOSTAT, 2020). Most countries in this continent have their own distinctive cultivation practices that have evolved in relation to the suitability of local climatic conditions and topography for potato cultivation; these practices, in turn, have impacted on the population structure of the pathogen *Phytophthora infestans*, cause of potato late blight, the disease that most limits yield (Dey et al., 2018; Fry et al., 2015).

Potatoes are cultivated year-round in western China, Myanmar, and the highlands of Thailand and Vietnam. In the northern and north-eastern hills of India, central China, Indonesia, the Philippines, and Korea, there are two annual cropping seasons, while in the plains of India, northern China, Japan, major parts of Vietnam, Pakistan, and Bangladesh, a single potato crop is grown annually during the winter where temperatures remain under 25 °C (Chen & Qu, 2008; Dey et al., 2018; Drenth & Sendall, 2004). The major potato-growing

regions are concentrated in eastern Asia, China, and the Indian subcontinent. Potatoes in this region are typically a cash crop rather than a staple and are cultivated mostly on small marginal farms by resource-poor farmers, whose socioeconomic condition is directly impacted by crop losses (Fry, 2016).

The history of late blight in Asia goes back more than 100 years (Butler, 1918; Ristaino & Hu, 2009; Saville & Ristaino, 2020). Since the 1980s, studies of the *P. infestans* populations in a number of Asian countries have been undertaken by various research groups. The impetus for these studies was provided by worldwide pathogen migrations, which started in the last quarter of the 20th century and have led to rapid population changes associated with serious late blight outbreaks in many Asian countries. However, the depth and scope of the knowledge of *P. infestans* populations is very varied (Fry, 2020). While there is almost no published information for most of the central Asian countries, there have been significant studies in countries including India, China, and Japan. In 2014, a late blight network for Asia, AsiaBlight, was initiated to promote national and international cooperation with the ultimate goal of improving sustainable late blight control (www.asiablight.org). Since 2015, as a first step in improving late blight management, the AsiaBlight network has been working under the auspices of the International Potato Center (CIP) to produce a coarse-scale map of the *P. infestans* population across Asia, using the approach pioneered by EuroBlight: a standardized genotyping based on 12-plex SSR (simple-sequence repeats) analysis, with use of a common database and mapping (Cooke et al., 2017). To date, only preliminary results of this mapping project are available. To complement this initiative, this review brings together previously published results on *P. infestans* in Asia and considers the history of these migrant populations, their distribution, and the changes in population structure in the major Asian potato-producing countries. In this way, we endeavour to improve late blight management and to indicate where increased phytosanitary regulation and improved quarantine efforts are required.

2 | MARKERS USED IN INVESTIGATIONS OF *P. infestans* IN ASIA

A range of genotypic and phenotypic markers have been used in the study of *P. infestans* worldwide to elucidate population structure, evolutionary history, and origin. These markers, reviewed by Cooke and Lees (2004) and Fry (2016), provide different levels of information and it is not always easy to compare results over time and space. *P. infestans* population studies started by analysing mating type and virulence to the 11 major resistance genes introgressed from *Solanum demissum*. From the 1980s, resistance to the phenylamide fungicide metalaxyl provided an additional tool, which also had practical significance for late blight control (Gisi & Cohen, 1996). Allozymes (Tooley et al., 1985) provided the first neutral, codominant markers, but had limited ability to discriminate between pathogen genotypes. Subsequently, use of the restriction fragment length polymorphism (RFLP) marker RG57 (Goodwin et al., 1992) and mitochondrial DNA (mtDNA) haplotype (Carter et al., 1990; Griffith & Shaw, 1998) allowed more detailed population analysis.

Variation for virulence may occur within asexual progeny of individual *P. infestans* isolates (Abu-El Samen et al., 2003); isolates identical in terms of other population markers may have highly variable virulence spectra (Guo et al., 2009). Because of this variability, which is influenced by host and environmental conditions (Andrivon et al., 2011), virulence phenotype has proved less effective than other markers in *P. infestans* population characterization and will only be touched on briefly in subsequent sections.

The advent of microsatellites or simple-sequence repeats (SSRs; Lees et al., 2006; Li et al., 2013a) provided neutral codominant markers that were less demanding than RFLPs in terms of the quantity and quality of pathogen DNA required, could be more readily automated, and were more discriminating. The adoption by the European late blight network, EuroBlight, of a standard set of 12 SSR markers that can be multiplexed has allowed readier comparisons of populations across Europe, and this has subsequently been extended to other geographic areas across the world, allowing the spread of multilocus genotypes (MLGs) to be mapped. The term clonal lineage is often used when referring to MLGs and their variants, which have a common origin but have accumulated minor allelic mutations. Defining and comparing genotypes using SSR is not always straightforward: the sizing of alleles may vary between laboratories depending on the precise technique adopted, the equipment, and the software used for analysis. For this reason, we advocate standardization via the use of reference isolates or DNA samples. In addition, the process of defining genotypes involves a degree of empiricism; discriminating between a variant within a genotype and a different genotype depends on knowledge of the variability of specific SSR markers. An objective examination of Bruvo's genetic distance data indicates thresholds of 0.05 are typical within lineages of relatively recent (<10 years) origin (Li et al., 2013a), increasing to 0.19 amongst isolates of significantly older lineages, such as US-1, in which many mutations have accumulated over countless generations (Martin et al., 2019). The average between-lineage genetic distance amongst an international collection of isolates was 0.433 (Martin et al., 2019). Nonetheless, information about populations of *P. infestans* across the world is rapidly increasing. With the inception of AsiaBlight, it is timely to review the published information on the population structures of *P. infestans* in the major potato-growing regions in southern and eastern Asia.

3 | ORIGINS OF *P. infestans* POPULATIONS IN ASIA

Phytophthora infestans originated in the Americas; both central Mexico (e.g., Wang et al., 2017) and the South American Andes (e.g., Martin et al., 2016) have been proposed as its centre of origin. Investigations using DNA obtained from historic herbarium late blight samples have revealed multiple intra- and intercontinental migrations of the pathogen. A distinct mitochondrial lineage HERB-1 was found in historic herbarium samples from 1845–1877 in Europe

and this is thought to have caused the Irish potato famine of the 1840s (Yoshida et al., 2013, 2014). HERB-1 belongs to the mtDNA Ia haplotype, to which it is assigned using the Griffith and Shaw (1998) haplotyping protocol, but sequencing the entire mitochondrial genome reveals it as a distinct subgroup (Martin et al., 2014). Subsequent study of historic late blight samples from Europe and America using SSRs identified the presence of a specific MLG that Saville et al. (2016) named FAM-1; this was associated with the mtDNA haplotype HERB-1 (Saville & Ristaino, 2020). FAM-1 had a panglobal distribution and caused widespread outbreaks in the USA, Europe, Africa, Asia, and Oceania during the 19th and the first half of the 20th century (Ristaino, 2020a; Saville et al., 2016; Saville & Ristaino, 2020). Ristaino (2020b) and Saville and Ristaino (2020) reported the presence of FAM-1 in a number of Asian countries in the first half of the 20th century between 1901 (Japan) and 1954 (Nepal).

The 20th century's most widespread lineage, named US-1 by Goodwin et al. (1994), was originally thought to have been responsible for the late blight epidemics in North America and Europe in the 1840s, but is now known to have been preceded by the lineages described above and to have emerged in the mid-20th century (Saville et al., 2016). US-1 (as defined by RG57 fingerprint, mating type, allozymes, and mtDNA) was reported from many potato-growing countries in Asia from the mid-20th century onwards. During the late 20th century another major change in *P. infestans* populations worldwide was observed when the presence of the A2 mating type was reported for first time outside Mexico, first in Europe (Hohl & Iselin, 1984), then in North America (Deahl et al., 1991) and Asia, for example, India in 1986 (Central Potato Research Institute, 1986). From the 1990s, the *P. infestans* population in Asia became more complex as the so-called "old" US-1 population was gradually replaced by the "new" population (sensu Spielman et al., 1991). The literature on the populations in selected major potato-producing countries of Asia is reviewed in detail below.

4 | COUNTRY PROFILES

These are ordered geographically from east to west.

4.1 | Japan and South Korea

Late blight was first reported in Japan in 1900, and the earliest samples analysed were herbarium specimens collected in 1901 and 1931; these were initially reported to possess the Ia mtDNA haplotype (Guo et al., 2010; Ristaino & Hu, 2009), but recently both have been assigned to the FAM-1 lineage with mtDNA HERB-1 (Ristaino, 2020b; Saville & Ristaino, 2020). However, when investigation of the population structure of *P. infestans* in Japan began, in 1987 (Akino et al., 2014), both mating types were detected (Mosa et al., 1989) with A2 predominating (68% of 207 isolates). These belonged to two genotypes, an A1 mtDNA Ib genotype identical to US-1 (therefore different from the 1901 and 1931 herbarium specimens), and a new A2 mtDNA IIa genotype, designated JP-1 (Akino et al., 2014; Koh et al., 1994). It is not clear when the US-1 genotype was introduced to Japan, but during the late 1980s and early 1990s it was displaced by JP-1, which became dominant first in Hokkaido, the northern island of Japan and the main potato-growing region, and then elsewhere in Japan (Kato et al., 1998; Mosa et al., 1989). Most isolates of JP-1 were intermediate in sensitivity to metalaxyl, although metalaxyl-sensitive and -resistant isolates of this genotype were also detected (Akino et al., 2014; Gotoh et al., 2005).

From 1996, A1 populations were again identified in Japan, but the US-1 genotype has not been detected since the 1990s (Akino, 2020). The new A1 genotypes were later classified as JP-2, JP-3, and JP-4, all having mtDNA IIa, distinct RG57 fingerprints, and being intermediate or resistant in terms of metalaxyl sensitivity (Gotoh et al., 2005, 2007). JP-1 also occurred in other Asian countries, including Korea and Indonesia (Gotoh et al., 2005); Koh et al. (1994) speculated that this genotype had originated in Mexico, but concluded that its migration route was unclear. The JP-2 genotype appeared identical to SIB-1, previously reported from Russia (Elansky et al., 2001); it has also been found in China (Akino et al., 2004, 2014), South Korea, and Thailand (see below) and closely resembles genotypes found in some European countries (Akino et al., 2010). This widespread genotype may have been introduced to Japan in the 1990s, perhaps from Europe (Akino et al., 2014). JP-3 is restricted to Japan and may have developed through sexual reproduction between JP-1 and JP-2, while JP-4 shares some SSR loci with Chinese and European genotypes and may have also originated outside Japan, possibly in Europe (Akino et al., 2014). After its first detection in 2001, JP-4 increased in frequency and, in 2004, became the dominant genotype in Japan (Akino et al., 2014). Thus, since the 1980s, the Japanese *P. infestans* population has consisted of a limited number of clonal genotypes and has undergone repeated genotype displacements. Most of these genotypes are thought to have been introduced from other countries, despite the limited importation of fresh potatoes to Japan and the country's geographical isolation; however, their migration routes are currently unknown (Akino et al., 2014).

Documentation of the South Korean *P. infestans* population is limited before the 1990s, but studies since 1991 show that it shares genotypes with Japan and has undergone similar major upheavals. Koh et al. (1994) reported that all but one of 57 isolates collected from South Korea in 1991 were A2 mating type belonging to the JP-1 genotype, while the single A1 isolate was US-1. Similarly, 16 isolates from 1992 characterized by Nishimura et al. (1999) and Gotoh et al. (2005) were all A2; these were assigned either to JP-1 or KR-1 (which differed from JP-1 only by a single RG57 band). The JP-1 population in South Korea exhibited diversity with respect to metalaxyl resistance, with both resistant and sensitive isolates being detected (Koh et al., 1994; Nishimura et al., 1999). During 1998–2000, the frequency of the A1 mating type increased to approximately 90%, with a concomitant decrease in the frequency of the A2 mating type (Hahm & Kim, 2001); these isolates were not tested for metalaxyl resistance. The dominance of A1 types (92%) was also reported in a

subsequent study of 367 isolates collected in 2002–2004 by Zhang et al. (2006). Among their isolates, three A1 genotypes were identified; the majority (67%) were assigned to JP-1, but as these were A1 mating type, they should probably have been assigned to JP-2. The remaining A1 isolates (24%) were mostly assigned to US-17, while a few belonged to a new genotype that Zhang et al. (2006) designated KR-1 (this genotype appears unrelated to the A2 KR-1 genotype of Gotoh et al., 2005). The A2 isolates were assigned to either the JP-1 or US-14 genotypes (Zhang et al., 2006). Thus, in South Korea, as in Japan, the A2 JP-1 genotype was displaced by the A1 JP-2 in the early 2000s. A recent study by Choi et al. (2020) shows continuing dominance of the population by A1 genotypes. They investigated the South Korean *P. infestans* population using SSR markers to genotype 172 isolates collected between 2009 and 2016, and identified four clonal lineages, KR_1_A1, KR_2_A2, SIB-1, and the A1 US-11. The KR_1_A1 genotype identified by Choi et al. (2020) could possibly be the same as KR-1 designated by Zhang et al. (2006), but there are insufficient genotypic markers common to the two studies to determine this. The A2 genotype KR-1 of Gotoh et al. (2005) could be related to KR_2_A2, which Choi et al. (2020) consider to be a minor variant of JP-1. US-11 was first found in 2014 and its frequency has increased since then; it was codominant with KR_1_A1 in 2014–2016 (Choi et al., 2020).

4.2 | China

China, the largest country in Asia and now the world's largest producer of potatoes, has four distinct potato cultivation zones. Northern China (Hebei, Jilin, Heliongjiang, Liaoning, Inner Mongolia, Ningxian, Huizu, Gansu, Qinghai, and Xinjiang provinces), where one potato crop is grown each year between May and October, constitutes half of China's total potato cultivation area. In south-western China (Sichuan, Guizhou, Chongqing, and Yunnan provinces), potatoes are cultivated year-round in small fields, which constitute 35% of the potato cultivation area. Central China (Jiangxi, Zhejiang, Anhui, Jiangsu, Shandong, Beijing, southern Hebei, Shaanxi, Shanxi, and southern Hunan provinces), where two crops are grown in the spring and autumn, constitutes 10% of China's total potato cultivation area. Southern China (Guangxi, Guangdong, and Fujian provinces) accounts for 5% of the total area and both major hosts of *P. infestans* are cultivated, potatoes in the winter and tomatoes in the spring (Chen & Qu, 2008; Zhu et al., 2016). The differences in cultivation practices, together with movement of host material within the country and introduction of genotypes from external sources, impact the disease cycle as well as the population structure of *P. infestans* in China in a way similar to that in India (Dey et al., 2018).

The earliest reported outbreaks of late blight in China occurred in the late 1930s when they caused considerable economic losses in south-western China (Guo et al., 2010). Study of herbarium specimens from this time has detected the presence of the FAM-1 genotype in specimens from 1938 and the 1940s and also of US-1 in another herbarium specimen from 1940 (Saville & Ristaino, 2020). In subsequent years, the US-1 genotype was detected from nationwide outbreaks in the 1950s (from south-western China in 1952 and northern China in 1954 and 1956; Guo et al., 2010), in pre-1982 isolates by Koh et al. (1994), and in a 1982 isolate from the wild species *Solanum lyratum* (Guo et al., 2010).

During the 1990s, changes in China congruent with worldwide upheavals in *P. infestans* populations (i.e., old US-1 population replaced by new populations) were reported (Gotoh et al., 2005; Guo et al., 2010; Nishimura et al., 1999). This was evidenced by the identification of the A2 mating type, first in 1995 from northern China (Zhang et al., 1996), subsequently from northern, south-western, and central China in 1995–1998 (Zhang et al., 2001), and by the detection of metalaxyl resistance among A1 isolates from northern China (Gotoh et al., 2005; Nishimura et al., 1999).

Multiple studies on Chinese isolates collected during 1996–2009 showed ongoing changes. During 1996–1997, A1 types (mtDNA Ia or IIa) were dominant in almost every potato-growing region of China, with A2 types being reported in low proportions from southern and central China (Gotoh et al., 2005). Gotoh et al. (2005) identified eight A1 and two A2 MLGs, of which two were also found outside China. One of these, the A1 mtDNA IIa SIB-1/JP-2, found in northern and central China, also occurred in Siberia (Elansky et al., 2001) and Japan (Gotoh et al., 2005) while the A2 mtDNA Ia TH-1, found in south-western China, also occurred in Thailand and Nepal. The other eight MLGs, CN-1 to CN-8, were newly defined, distributed in different parts of the country (Figure 1) and were exclusive to China; all were mtDNA Ia, seven A1 and one A2 (CN-3) (Gotoh et al., 2005). Guo et al. (2009) studied isolates collected during 1998–2001 in northern China; all had identical SSR genotypes and were A1 mtDNA IIa, so may have belonged to the SIB-1/JP-2 lineage, but as the markers previously used to define this genotype were not employed in this study, this cannot be confirmed.

Guo et al. (2010) found regional differences in population structure in a study of 100 isolates collected between 1998 and 2004, with overall dominance of A1 metalaxyl-resistant populations. Seven genotypes were identified, namely US-1, US-16 (A1/mtDNA IIb), MO-6 (A1/mtDNA Ia; previously identified from Moscow, Elansky et al., 2001), SIB-1/JP-2, and new Chinese genotypes CN-9 (A2), and CN-10 and CN-11 (both A1). Genotype SIB-1/JP-2 and variants predominated and were widely distributed in both northern China and south-western China (Sichuan and Yunnan), indicating spread within the country possibly from north to south in seed potatoes. South-western China, where potatoes are grown year-round in small fields, was the most genotypically diverse region with seven clonal genotypes plus variants representing both mating types and all four mtDNA haplotypes. Guo et al. (2010) hypothesized that such diversity indicated the likelihood of multiple migrations of *P. infestans* into China after the initial introduction in the 1930s. US-1 variants were found in very low frequency from potato and tomato crops in south-western and central China (Guo et al., 2010; Figure 2). The genotypes US-16 and CN-11 (both A1, mtDNA IIb) were found in southern China during 1998–2004 (Guo et al., 2010); A1 mtDNA IIb types were also reported from the same region in 1998–2007 by Li et al. (2009) and in 2004–2009 by Li et al. (2013b).

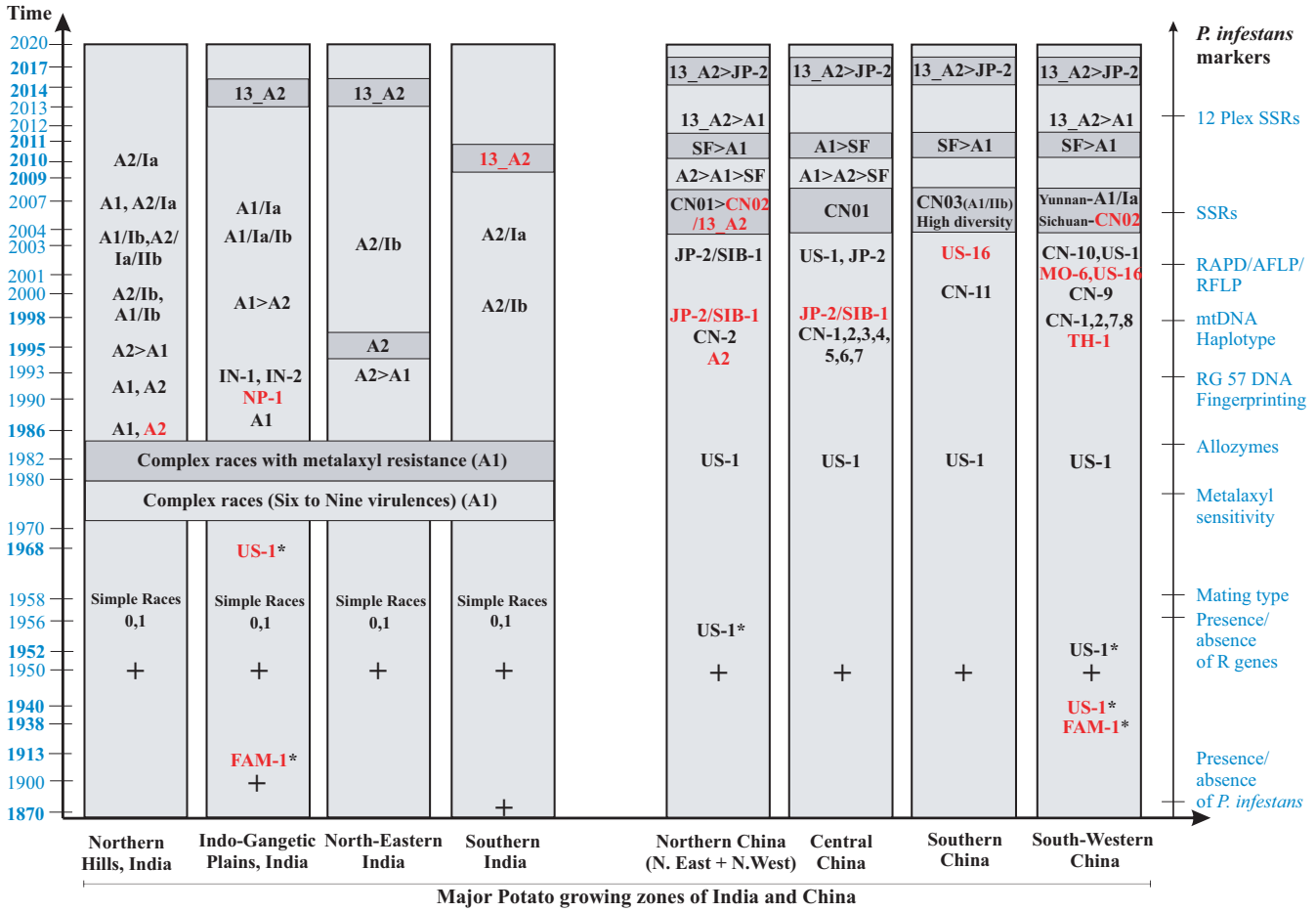

FIGURE 1 Schematic representation of the changes in *Phytophthora infestans* genotypes in India and China, from first reports in the 1870s to 2020. First findings of genotypes in the respective potato-growing zones are shown in red. Shaded horizontal boxes within zones indicate major changes in population structure. Years in bold font denote time scales during which major events influencing population changes took place. '>' indicates the frequency of one type is greater than the other type for that given period. Findings from later analysis of herbarium specimens are marked *. The presence of *P. infestans* in the absence of any other information is indicated by +. Details of multilocus genotypes are given in Table 1 [Colour figure can be viewed at wileyonlinelibrary.com]

The increasing use of SSRs for population characterization complicates comparison of published literature on population studies of *P. infestans* in China after 2010 with those carried out before that date and with those in other countries. This is primarily due to the use of different combinations of markers and lack of standardization in allele calling as well as limited within-country coordination. For example, the allele nomenclature used by Tian et al. (2015a) differed from that of Li et al. (2013a, 2013b) in the use of the D13 locus; and Zhu et al. (2015) used older SSR loci with only four in common with the 12-plex assay of Li et al. (2013a). However, the continuing use of mtDNA haplotyping indicates that the US-1 genotype (mtDNA Ib) has not been identified in studies published since 2010 (e.g., Li et al., 2013b; Tian et al., 2015a); the report of US-1.3 in 2004 by Guo et al. (2010) appears to be the most recent finding.

Regional differences were found in further countrywide studies with 188 isolates from 2004–2009 detected using SSR markers (Li et al., 2013b). Three dominant clonal lineages, namely CN01 (mtDNA IIa), CN02 (mtDNA Ia), and CN03 (mtDNA IIb) were associated with northern China, south-western China, and southern China, respectively (note, this nomenclature is distinct from the earlier naming of genotypes CN-1 etc., begun by Gotoh et al., 2005). CN02 was notable as this A2 genotype was shown to be part of the aggressive European 13_A2 (Blue_13) lineage; it was first identified in an isolate from Yunnan province (south-western China) collected in 2005 (Li et al., 2013b), only a year after the earliest known 13_A2 isolate was collected in Europe (Cooke et al., 2012). This genotype was dominant in south-western China in 2005–2009 but occurred in lower frequency in central and northern China (Li et al., 2013b). The CN01 lineage of northern China probably belonged to the same A1 mtDNA IIa lineage previously named as SIB-1/JP-2, which was the dominant genotype in previous years 1998–2004 (Guo et al., 2009, 2010). The CN03 lineage showed a high level of subclonal variation and Li et al. (2013b) hypothesized that this was an older, less aggressive lineage, which had survived because of regional isolation. This lineage may be the same one to which the A1/mtDNA IIb genotypes US-16 and CN-11, found in southern China by Guo et al. (2010), belonged. Tian et al. (2015a) showed that the *P. infestans* population in central China (northern Shaanxi) in 2009 had low

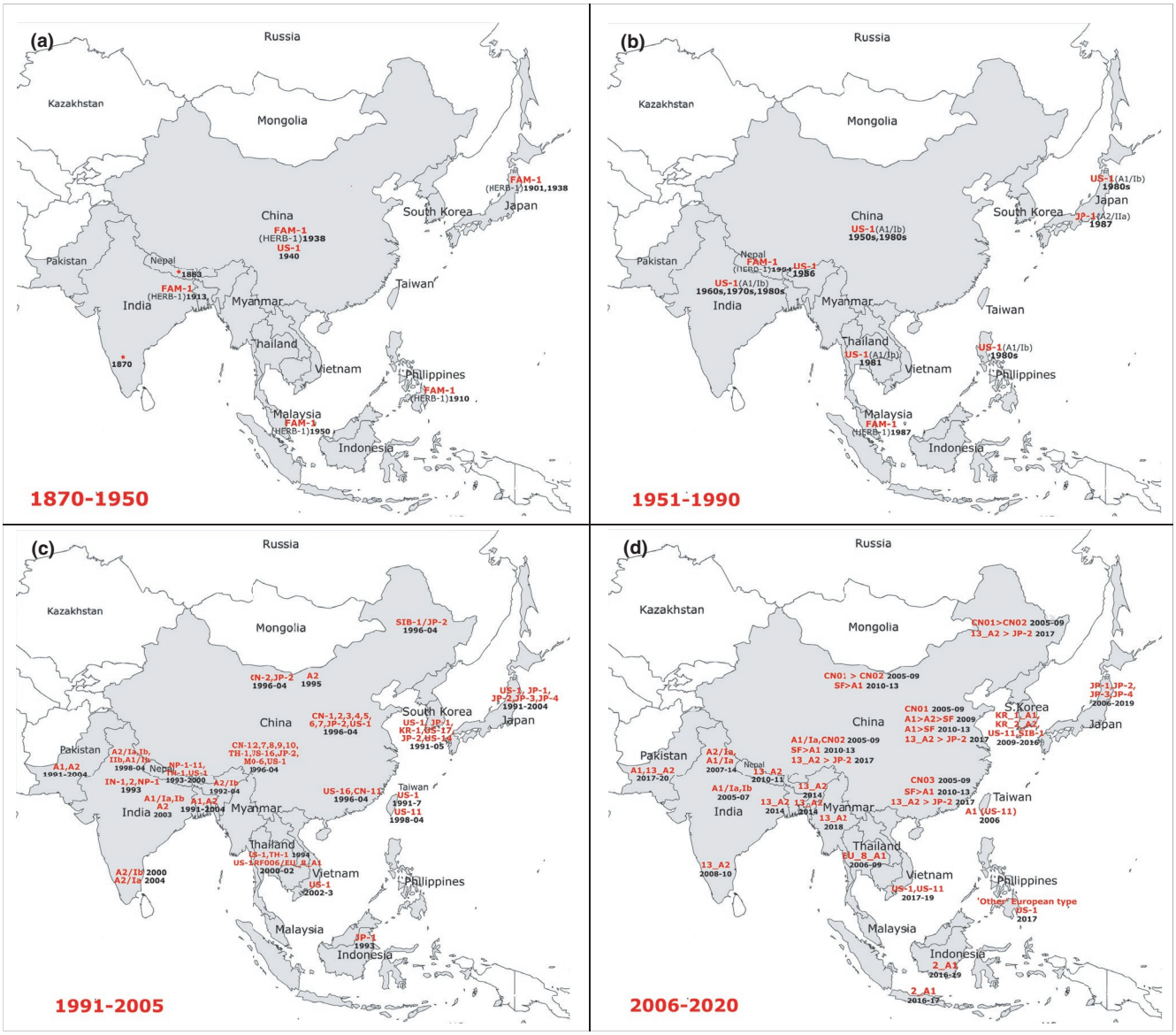

FIGURE 2 *Phytophthora infestans* populations present in the major potato-growing regions of Asia from (a) 1870–1950, (b) 1951–1990, (c) 1991–2005, and (d) 2006–2019. Multilocus genotypes, mating types, mitochondrial haplotypes, and years studied are indicated where these have been reported. The presence of *P. infestans* is indicated by *. '>' indicates that the frequency of one type is greater than the other type for a given period. The political boundaries and geographic names shown on the map are for indicative purposes only: the authors remain neutral with respect to any jurisdictional claims [Colour figure can be viewed at wileyonlinelibrary.com]

genetic diversity and was dominated by A1 (97% of total isolates); this population may have derived from the northern China population studied by Guo et al. (2009) and may belong to the CN01 lineage of Li et al. (2013b).

In the last 10 years (2009–2019), a number of studies have reported rapid changes in the *P. infestans* population, with an increase in the occurrence of A2 and self-fertile isolates in most regions except central China where the A1 mating type has remained dominant (Tian et al., 2015b, 2016; Zhu et al., 2015, 2016). Tian et al. (2016), in a study of 959 isolates, showed that in north-western China between 2009 and 2011, the frequency of first A2 and then self-fertile isolates increased. Phylogeny analysis indicated two clusters; Cluster I contained mostly A1 isolates with mtDNA IIa, Cluster II contained the majority of A2 and self-fertile isolates with mtDNA Ia, but these were not considered to belong to the CN02/13_A2 lineage found by Li et al. (2013b) in 2009. Tian et al. (2016) did not detect any oospores during examinations of hundreds of diseased leaves and concluded that the population was reproducing clonally; the major population upheavals between these years were attributed to long-distance migration probably in seed tubers. Similarly, Tian et al. (2015b), in a study of 279 isolates of *P. infestans* from a potato germplasm nursery in north-western China (Ningxia), found A1, A2, and self-fertile types in 2010, but only A2 and self-fertile isolates in 2011.

Zhu et al. (2015) reported a dominance of self-fertile isolates in southern China (Fujian) in 2010–2012 and concluded that *P. infestans*

TABLE 1 Genotypes of *Phytophthora infestans* identified in Asia

Multilocus genotype	Year	Mating type	Mitochondrial haplotype	Country[a]	Reference[a]
CN-1, -2, -4, -5, -6, -7, -8	1996–1997	A1	Ia	China	Gotoh et al. (2005)
CN-3	1996–1997	A2	Ia	China	Gotoh et al. (2005)
CN-9	2001	A2	Ia	China	Guo et al. (2010)
CN-10	2004	A1	Ia	China	Guo et al. (2010)
CN-11	2000, 2002	A1	IIb	China	Guo et al. (2010)
CN01	2004–2009	A1	IIa	China	Li et al. (2013a)
CN03	2004–2009	A1	Ia/IIb	China	Li et al. (2013a)
FAM-1	Before 1950	Presumably A1	Ia (HERB-1)	Japan, Philippines, India, China, Malaysia, Nepal	Ristaino (2020b); Saville and Ristaino (2020)
IN-1	1993	A1	Ia	India, Nepal	Gotoh et al. (2005)
IN-2	1993	A1	Ia	India	Gotoh et al. (2005)
JP-1	Late 1980s onwards	A2	IIa	Japan, Korea, Indonesia	Koh et al. (1994); Gotoh et al. (2005)
JP-2/SIB-1/RF006	1996 onwards	A1	IIa	Japan, China, Korea, Thailand	Akino et al. (2004, 2014); Guo et al. (2009); Guo, M., personal communication; Zhang et al. (2006); Petchaboon et al. (2014)
JP-3	1996 onwards	A1	IIa	Japan	Gotoh et al. (2005); Akino et al. (2014)
JP-4	1996 onwards	A1	IIa	Japan	Akino et al. (2014)
KR-1	1992	A2	IIa	Korea	Gotoh et al. (2005)
KR_1_A1	2009–2016	A1	-	Korea	Choi et al. (2020)
KR_2_A2	2009–2016	A2	-	Korea	Choi et al. (2020)
KR-1	2002–2004	A1	IIa	Korea	Zhang et al. (2006)
MO-6	2004	A1	Ia	China	Guo et al. (2010)
NP-1	1993, 1996–1997	A1	Ia	India, Nepal	Gotoh et al. (2005)
NP-2	1997	A1	Ia	Nepal	Gotoh et al. (2005)
NP1	1999–2000	A1	Ia	Nepal	Ghimire et al. (2003)
NP2	1999–2000	A1&A2	Ia	Nepal	Ghimire et al. (2003)
NP3/US-1	1999–2000	A1	Ib	Nepal	Ghimire et al. (2003)
NP4, 5, 7, 9	1999–2000	A1	Ia	Nepal	Ghimire et al. (2003)
NP6	1999–2000	A1	-	Nepal	Ghimire et al. (2003)
NP8	1999–2000	A2	Ib	Nepal	Ghimire et al. (2003)
NP10, 11	1999–2000	A2	Ia	Nepal	Ghimire et al. (2003)
Self-fertile types	2009–2013	Self-fertile	-	China	Zhu et al. (2016); Tian et al. (2015b)

(Continues)

TABLE 1 (Continued)

Multilocus genotype	Year	Mating type	Mitochondrial haplotype	Country[a]	Reference[a]
TH-1	1994, 1997	A2	Ia	Thailand, China, Nepal	Gotoh et al. (2005)
Unknown	1996–2003	A2	Ib	India	Chimote et al. (2010)
US-1	1940–2000	A1	Ib	China, India, Nepal, Japan, Taiwan, Thailand, Vietnam	Saville and Ristaino (2020); Ristaino and Hu (2009); Guo et al. (2010); Chimote et al. (2010); Ghimire et al. (2003); Akino et al. (2014), Chen et al. (2009); Gotoh et al. (2005); Le et al. (2008)
US-11	1998–2016	A1	IIb	Taiwan, Korea, Vietnam	Chen et al. (2009); Choi et al. (2020); D.E.L. Cooke, unpublished
US-14	2002–2003	A2	IIa	Korea	Zhang et al. (2006)
US-16	2002, 2004	A1	IIb	China	Guo et al. (2010)
US-17	2003–2004	A1	IIa	Korea	Zhang et al. (2006)
2_A1	2016–2019	A1	Ia	Indonesia	Dangi et al. (2021); L.R. Cooke, unpublished
13_A2/CN02	2005–2019	A2	Ia	China, India, Bangladesh, Nepal, Pakistan, Myanmar	Li et al. (2013b); Chowdappa et al. (2015); Dey et al. (2018); Islam et al. (2020); Adhikari (2017); Raza et al. (2020); D.E.L. Cooke, unpublished

[a]Within genotypes, the countries and their associated citations are ordered chronologically by the first reported occurrence of that genotype in each country.

was mainly reproducing clonally. As most seed tubers were imported into this region, like Tian et al. (2016), Zhu et al. (2015) considered that these dramatic changes in the population structure were attributable to movement of the pathogen in infected seed. Zhu et al. (2016) studied 2,250 *P. infestans* isolates collected from fields in northern, central, south-western, and southern China between 2010 and 2013. All isolates in this study were either A1 or self-fertile; surprisingly no A2 isolates were detected. Self-fertile isolates dominated in the northern, south-western, and southern regions, while A1 isolates were dominant in central China.

In contrast to the findings of Zhu et al. (2016), studies of the *P. infestans* population in northern China (Heilongjiang) over a 14-year period (2005–2019) found that while the A1 genotype SIB-1/JP-2 was dominant before 2010, the frequency of 13_A2 increased from 2011 to 2013, although it was not found in 2015–2016 (M. Guo, Heilongjiang Academy of Agricultural Sciences, China, 2020, personal communication). In south-western China (Yunnan) the 13_A2 genotype became dominant after 2012 (Cao et al., 2020); Liang et al. (2020) detected 13_A2 in Yunnan in 2013–2015, but not in 2016–2017. Zhang et al. (2020) reported that among 687 isolates collected from eight Provinces across China in 2015–2017, 13_A2 was dominant (77% of isolates) and the remainder belonged to the SIB-1 lineage.

Thus, studies of the *P. infestans* population in China indicate repeated introductions, starting with mtDNA Ia types (probably of the FAM-1 lineage) in the late 1930s followed by the A1 mtDNA Ib US-1 at some point before 1982. From the mid-1990s, as elsewhere in the world, there were major migrations during which the A2 mating type was detected for the first time in China (1995), but it remained at a relatively low frequency for the next 10 years. These introductions led to clear regional differentiation within China with the A1 mtDNA IIa SIB-1/JP-2/CN-3/CN01 lineage predominating in northern China, the A1 mtDNA IIb US-16/CN-11/CN03 lineage in southern China, and a genetically diverse population in the multicropping south-western region. In 2005 the aggressive European 13_A2 lineage was first detected in south-western China and this A2 genotype dominated the population in that region in 2005–2009. After 2009, the incidence of self-fertile isolates increased, and published papers indicate ongoing major population upheavals with both regional and temporal differences, which may be associated with seed potato production and movement. Contrasting results from different studies may be indicative of these upheavals but may also be associated with differences in sampling strategies and characterization techniques, emphasizing the need for cooperation between research groups.

4.3 | Taiwan

The island of Taiwan, off the coast of Fijian, southern China, grows potatoes as a winter crop (October–February) and tomatoes in the spring, summer, and winter, with the greatest area of tomato production being the lowland winter crop. Late blight was first reported in Taiwan on both potato and tomato in the early 1900s (Ann et al., 1998), predating reports from mainland China. To date, it does not appear that any herbarium specimens from these early outbreaks have been examined. Until the late 1990s, although it often caused serious losses of the spring and summer tomato crops grown in the highlands, late blight on the winter-grown potato and tomato crops in the lowlands occurred only sporadically and was not a major problem (Chen et al., 2008). Studies of *P. infestans* in Taiwan during the early 1990s (the vast majority from tomato with a few from potato) showed that the population was A1 mating type, mtDNA Ib, metalaxyl-sensitive, and belonged to the US-1 genotype (Ann et al., 1998; Griffith & Shaw, 1998; Hartman & Huang, 1995; Koh et al., 1994). However, from 1997 to 1998, metalaxyl-resistant strains of *P. infestans* began to cause severe losses to winter-grown potatoes and tomatoes in addition to spring- and summer-grown tomatoes. Deahl et al. (2002) and Jyan et al. (2004) studied 139 isolates of *P. infestans* collected in 1991–2001 and 97 isolates collected in 1992–2002, respectively, and showed a major population shift from an exclusively US-1 population in 1991–1997 to an almost exclusively US-11 population after 1999. The metalaxyl-resistant A1 US-11 genotype, which was first detected in Taiwan in 1998, might have been imported from the USA (where US-11 had been first identified in 1993; Miller et al., 1997) in infected potatoes (Deahl et al., 2002; Jyan et al., 2004). Because of this population change, metalaxyl was removed from the list of recommended fungicides in Taiwan (Deahl et al., 2002).

By 2006, the introduced US-11 genotype had totally displaced the old US-1 genotype and the population had become completely metalaxyl-resistant, although still exclusively A1 mating type (Chen et al., 2008, 2009). Deahl et al. (2008) reported that two isolates obtained from tomato during 2004 and 2006 were A2 mating type, although their other characteristics were typical of the US-11 genotype. However, this finding was disputed by Ann et al. (2010) who reported that further testing of these isolates and others from the same vicinity showed that all were of the A1 mating type. Since 2010, there do not appear to be any published papers on the *P. infestans* population in Taiwan in the scientific literature, although genotyping of pathogen DNA within the AsiaBlight coarse-scale mapping project from sampling in 2019 indicates the presence of US-11 (D. E. L. Cooke, unpublished data).

4.4 | South Asian countries

Potatoes were introduced to South Asian countries (notably Indonesia, the Philippines, and Vietnam) by Europeans in the 18th and 19th centuries. In the latter part of the 20th century potato production in South Asia became increasingly important and it was estimated that every year late blight caused 15%–20% yield loss (Drenth & Sendall, 2004). However, relatively little is known about the *P. infestans* population structure in these countries and even the date of the arrival of late blight is poorly documented. The FAM-1 genotype was identified in late blight herbarium specimens of 1910 and 1950,

collected from the Philippines and Malaysia, respectively, but the US-1 genotype was found in a tomato late blight specimen collected from Thailand in 1981 (Saville & Ristaino, 2020). The FAM-1 genotype was again identified in 1987 in Malaysia from tomato (Saville & Ristaino, 2020).

From the mid-1990s, the presence of both old US-1 and new genotypes was reported. Nishimura et al. (1999) and Gotoh et al. (2005) identified the presence of the A2 mating type in Indonesia and Thailand in 1993 and 1994, respectively. In Chiang Mai, Thailand, in 1994, both A1 (US-1) and A2 metalaxyl-sensitive isolates were obtained from potato, but only A1 US-1 isolates from tomato (Nishimura et al.,1999). A new RFLP genotype with A2 mating type and Ia mtDNA haplotype from Thailand designated TH-1 was characterized by Gotoh et al. (2005), who reported that this genotype also occurred in other Asian countries including Nepal and southwestern China. A further shift in the *P. infestans* population on potato in Thailand was shown by Petchaboon et al. (2014), who studied 80 isolates of *P. infestans* collected in 2000–2002, 27 from potato and 53 from tomato, all of which were A1 mating type. All their isolates from tomato, with one exception, belonged to the US-1 clonal lineage, in agreement with Nishimura et al. (1999) and Gotoh et al. (2005). However, Petchaboon et al. (2014) reported that, with two exceptions, their isolates from potato were mtDNA IIa and had RG57 patterns that matched European lineages. Their predominant potato lineage, which they assigned to RF006 (Day et al., 2004), is identical to EU_8_A1, consistent with data from 2009 confirming the presence of EU_8_A1 in samples collected from potato in Thailand (R. de Boer and A.T. Slater, Agriculture Victoria, Australia, 2020, personal communication). This same lineage was probably also found by Jaimasit and Prakob (2010) who studied isolates collected from potato during 2006–2009; their isolates ($n = 117$) were all A1 mating type and mtDNA IIa and the majority were metalaxyl-sensitive, but -intermediate and -resistant isolates were also found.

In Vietnam, Le et al. (2008a) characterized 294 isolates obtained in 2002–2003 that were all A1; in a subset of isolates further characterized by mtDNA haplotype and RG57 fingerprinting, all closely resembled US-1. Therefore, Le et al. (2008a) concluded that the *P. infestans* population of Vietnam was still an old US-1 population, and, interestingly, metalaxyl-resistant isolates dominated the population in the south on both potato and tomato, although they were much less frequent in the north. Metalaxyl-resistant US-1 isolates are infrequent, but they had also been collected from Ireland in 1980 (Goodwin et al., 1996), and later in the Philippines (Koh et al., 1994) and South Africa (McLeod et al., 2001). By 2007, preliminary findings from a study of isolates indicated that the population in Vietnam had begun to change, but characterization was not reported (Le et al., 2008b). Genotyping of pathogen samples collected between 2017 and 2019 under the auspices of AsiaBlight is in progress: preliminary results indicate the continuing occurrence of US-1, but also the presence of US-11 types.

The *P. infestans* population in Indonesia has been very little studied until recently; Nishimura et al. (1999) reported on four isolates (all A2) collected in 1993 and two of these were further characterized by Gotoh et al. (2005) as JP-1. However, during 2016–2019, Dangi et al. (2021) collected 140 FTA card samples of *P. infestans* from the three main potato-growing areas of the island of Java, where 50% of Indonesia's potatoes are produced. The majority of these were assigned to the European genotype 2_A1, but there was a high level of subclonal variation and other genotypes including some unique types as well as other European types were also identified. In 2016–2017 FTA card samples were also collected in Java as part of the AsiaBlight coarse-scale mapping project, and of those samples that were successfully genotyped, all were assigned to genotype 2_A1 (L. R. Cooke, unpublished data).

There do not appear to have been any recent published studies of the *P. infestans* population in the Philippines, but FTA card samples were collected under the auspices of AsiaBlight in 2017. Those samples successfully characterized belonged to a single genotype possibly related to a European type, but distinct from that found in Indonesia (L. R. Cooke, unpublished data). US-1 was also identified from another sampling study conducted by Wageningen University & Research in 2017 (G. J. T. Kessel, Wageningen University & Research, Netherlands, 2020, personal communication).

4.5 | Nepal

Nepal has three major agroecological regions, the lowlands (Terai), the mid-hills, and the highlands; most potatoes are grown in the mid-hill region. Late blight was first reported in Nepal between 1883 and 1897 (Shrestha, 1976). A herbarium specimen of late blight collected from potato in Nepal in 1954 belonged to the FAM-1 lineage (Saville & Ristaino, 2020). Since the mid-1990s, late blight has caused severe crop losses, sometimes exceeding 75% in the highlands and 90% in the lowlands (Gaire et al., 2014), and fungicides were reported to have become less effective in controlling the disease (Ghimire et al., 2001) indicating that the *P. infestans* population in Nepal was changing. Shrestha et al. (1998) reported the first detection of the A2 mating type in Nepal among isolates from 1996 (6% of isolates) and its frequency increased to 42% in 1997; these authors speculated that the A2 mating type might have been recently introduced with potatoes from Latin America. Shrestha (2005) further reported on 158 isolates collected from potato- and tomato-growing areas between 1997 and 1999. All 15 isolates from tomato were A1 mating type, but in isolates from potato the A2 mating type predominated in the highlands, while in the mid-hills and lowlands A1 types were dominant; allozyme genotyping indicated that the A1 isolates were probably of the US-1 lineage, whereas the A2 isolates were a new population.

Ongoing changes were also investigated by Ghimire et al. (2001) who collected *P. infestans* isolates from potato crops in 1999 and 2000; the majority of isolates were A1 and metalaxyl-sensitive, although metalaxyl resistance occurred in both mating types. Ghimire et al. (2003) used RG57 fingerprinting and mtDNA haplotyping to characterize isolates from 1999–2000 and identified a total of 11 different RG57 genotypes, of which three constituted 94% of those analysed. Of the two most frequent genotypes (NP1, NP2, 68%

and 18% of the population, respectively), NP1 was an A1 mtDNA Ia type and NP2 was also mtDNA Ia but was associated with both mating types. Comparison of RG57 fingerprints indicated that neither NP1 nor NP2 was identical with the genotypes NP-1 or NP-2 defined by Gotoh et al. (2005) in isolates from 1996–1997. Ghimire et al. (2003)'s third most frequent genotype, NP3, which constituted 17.5% of characterized isolates, was identical to US-1. The remaining eight genotypes were each represented by between one and four isolates and included four unique genotypes (each found in only one isolate); Ghimire et al. (2003) speculated that this diversity may have resulted from multiple introductions of the pathogen into Nepal and from sexual recombination.

The *P. infestans* population in Nepal was not investigated further until 2010–2011, when Adhikari (2017) collected isolates from the three different ecological regions; these were 39% A1 and 61% A2 with the frequency of the A2 mating type being much greater in the highlands (88%) than the lowlands (12%), in agreement with Shrestha (2005). Metalaxyl-resistant and -intermediate isolates constituted 32% and 38% of those tested, respectively. SSR analysis of 19 selected A2 isolates representing the three ecological regions showed that all were 13_A2 (Adhikari, 2017). Further sample collection for genotyping from both potato and tomato was carried out in 2016–2017 as part of the AsiaBlight network; results of this are yet to be published.

4.6 | Bangladesh

Bangladesh is the third largest producer of potatoes in Asia (after China and India). Potato cultivation occurs in the winter months under climatic conditions similar to those of the east Indian state of West Bengal, which it borders. Late blight causes mean annual yield losses of up to 30% (Hossain et al., 2009). The occurrence of late blight in the region that subsequently became the country of Bangladesh was first reported in 1922 (Hossain et al., 2009), but relatively little information has been published on the *P. infestans* population. In 1995–1996, seven of 20 isolates tested were found to be metalaxyl-resistant (Hossain et al., 2009), while Forbes (2004) reported that both A1 and A2 mating types were present. Recently, in a project funded by the Netherlands Space Office Geodata for Agricultural and Water Program (G4AW), sampling starting in 2014 showed that the 13_A2 genotype was widespread in Bangladesh with multiple subclonal lineages (Islam et al., 2020; Kessel et al., 2017).

4.7 | India

Potatoes were introduced to India about 400 years ago, but only became a significant crop at the end of the 18th century (Shetty et al., 2014; Singh & Rana, 2014). The presence of late blight was first recorded in the late 19th century (Butler, 1918; Singh & Bhattacharya, 1999).

The oldest characterized herbarium late blight specimen, collected from eastern India (Bhagalpur) in 1913, belonged to the FAM-1 lineage, whereas specimens collected in 1968 and 1974 were the US-1 genotype, which had been introduced to India in the intervening period (Saville & Ristaino, 2020). During this time, breeding for late blight resistance in India had been ongoing, particularly after 1949 when a dedicated Potato Institute was opened in Shimla (Singh et al., 1999). From the 1960s, incorporation of field resistance was emphasized and, in parallel with the breeding effort, the pathogen was monitored for virulence to resistance (*R*) genes. Simple races were prevalent during 1958–1970 in the major potato cultivation areas of India, but complexity increased and by the 1990s, seven to eight virulence genes were observed in *P. infestans* isolates from almost all potato-growing regions in India (Singh & Bhattacharya, 1999; Figure 1). Severe late blight incidents occurred every year in the hill regions, but in the plains, where late blight had previously been sporadic, it became much more serious in the 1990s leading to enormous crop losses; Singh and Bhattacharya (1999) attributed this to changing weather conditions, but it may also have marked the start of a transition in the *P. infestans* population in India.

The first detection of the A2 mating type of *P. infestans* in India was in 1986 (Central Potato Research Institute, 1986), but regular monitoring for mating type was not started until 1990 (Singh & Bhattacharya, 1999). Between 1990 and 1993, Singh et al. (1994) collected 104 *P. infestans* isolates from the major potato-growing regions. All isolates from the plains were A1, but a mixed A1/A2 population was found in the northern and north-eastern hills where the frequency of the A2 mating type ranged from 5% to 60% (Singh et al., 1994). The frequency of the A2 mating type continued to rise in the hill regions, reaching 93% in the northern hills and approaching 100% in the north-east by 1995 (Singh & Bhattacharya, 1999). In the Indo-Gangetic Plains, the A2 mating type was not detected until 1997, but reached 50% frequency in 1997 and 1998 (Singh & Bhattacharya, 1999). Similarly, Atheya et al. (2005) reported that between 1992 and 1998 the hill regions were dominated by an A2 population, while in the plains A1 was more frequent than A2.

Metalaxyl was introduced commercially to control late blight in India in 1988 and metalaxyl-resistance in *P. infestans* was first encountered soon after in 1989 (Arora, 1991; Singh & Pundhir, 2013). Subsequent studies of the pathogen population often included testing for metalaxyl resistance.

A countrywide study between 1996 and 2006 reported that the A2 mating type dominated the populations in the temperate northern and north-eastern hills and in the South Indian hills, whereas the A1 mating type dominated in the subtropical Indo-Gangetic Plains (Chimote et al., 2010). The A2 isolates collected between 1996 and 2003 included both metalaxyl-resistant and -sensitive strains and, unusually, 55% were reported to possess the mtDNA Ib haplotype while the remainder were mtDNA Ia and IIb. The combination of the A2 mating type with the mtDNA Ib haplotype has apparently only been reported once before from the Netherlands (Li et al., 2012); whether its finding in India represents a link to the Netherlands is not known. In the northern hill state of Uttarakhand, the population

of *P. infestans* was first examined during 2005–2007; of only four isolates tested for mating type, all were A1 and metalaxyl-resistant (Singh & Pundhir, 2013). Sharma et al. (2016) characterized isolates collected between 2008 and 2010 from Himachal Pradesh, another northern hill state; all were A2 with mtDNA Ia and had intermediate resistance to metalaxyl, but whether this A2/Ia population belonged to the 13_A2 lineage was not reported. The trend for the frequency of the A2 mating type to increase over time in the northern hills of India parallels the situation noted in Nepal.

In 2008, 2009, and 2010, severe outbreaks of late blight on tomato occurred in the state of Karnakata in south-west India; before that time, late blight had not been considered a serious threat to tomato production in India. Nineteen isolates collected from infected tomato in 2009–2010 were all shown to belong to the 13_A2 lineage and it was concluded that introduction of this lineage to India was responsible for the epidemics on tomato (Chowdappa et al., 2013). A further study by Chowdappa et al. (2015) characterized 157 isolates collected in southern India (Karnakata, Tamil Nadu, and Andhra Pradesh) from potato (n = 63) and tomato (n = 94) between 2010 and 2012, and showed that all were A2, metalaxyl-resistant, belonged to the 13_A2 lineage, and were equally aggressive to potato and tomato. In 2014, a major late blight epidemic on potato in West Bengal (in eastern India, the second largest potato-producing state in India) resulted in crop losses so severe that they led to socioeconomic upheaval and were even associated with suicides among potato farmers (Fry, 2016). A detailed study of 59 isolates collected from eastern and north-eastern India in 2013–2014 (40 from potato, 19 from tomato) found that all belonged to the 13_A2 genotype; 24 subclonal variants within this genotype were identified, of which 19 were unique to this region (Dey et al., 2018). Comparison of the 13_A2 variants with those found elsewhere in India and in Europe suggested either multiple independent imports into different regions of India or local mutations resulting in highly diverse 13_A2 populations (Dey et al., 2018).

4.8 | Pakistan

Potatoes are a significant crop in Pakistan; over 95% of the production is in the Punjab province, which borders the Indian state of Punjab. Late blight was first reported in 1984 in Swat (Khan et al., 1985), and since then has been reported from the plains of the Punjab, the North-West Frontier Province (NWFP), Baluchistan, and northern Pakistan. The occurrence of both mating types in almost equal proportions was identified in 1994 in the Punjab and the NWFP; most importantly, both mating types occurred together in one field (Ahmad & Mirza, 1995). Subsequently, between 1997 and 2000, both mating types were found in all areas except the lower valleys of NWFP, where only A1 and self-fertile isolates were found (Ahmad et al., 2002a). When these isolates were tested for metalaxyl sensitivity, the frequency of intermediate isolates was greater than that of either sensitive or resistant isolates, regardless of mating type (Ahmad et al., 2002b). In 2003–2004, a further collection of *P. infestans* isolates from the Punjab, the Swat valley, and the Upper Swat valley provinces was tested for metalaxyl sensitivity and it was found that the frequency of metalaxyl-resistant isolates had increased among both A1 and A2 populations except in the Upper Swat valley, where resistance occurred only in the A1 population (Ahmad et al., 2008). Since these studies, published information on the population structure of *P. infestans* in Pakistan was lacking for more than 10 years. However, a recent study of isolates collected in 2017–2018 from six potato-growing districts of the Punjab showed that around 20% of the population was A2 mating type, and genotyping of samples collected in 2019–2020 under the auspices of AsiaBlight has identified the presence of genotype 13_A2 (Raza et al., 2020).

5 | DISCUSSION

The literature reviewed above makes it clear that the populations of *P. infestans* in the major potato-growing regions of Asia have repeatedly undergone major shifts since the first arrival of the pathogen in Asia in the late 19th century; the earliest reports of late blight being from India (1870–1880) and Nepal (1883, 1897). These outbreaks were most probably caused by the FAM-1 lineage, but by the 1950s this population had been replaced by A1 populations belonging to the US-1 clonal lineage, as revealed by analysis of herbarium specimens (Ristaino, 2020b; Ristaino & Hu, 2009; Saville & Ristaino, 2020) (Figure 2a). The US-1 clonal lineage was apparently dominant between 1960 and 1990, coinciding with the period when late blight became a focus of research in various Asian countries. This clonal lineage may still be present in low frequency in some countries, particularly on tomato; for example, it was detected in Taiwan in 2003 (Chen et al., 2009), and in Vietnam it was the dominant lineage in 2002–2003 (Le et al., 2008a).

Further major shifts in the Asian *P. infestans* population began in the late 1980s, as in other parts of the world, and are still ongoing. These introduced new genotypes of both mating types, which displaced the old US-1 population, and led to more diverse, but still predominantly clonal, populations across Asia (Figure 2b). Some of these population changes were strikingly rapid (e.g., in Taiwan). In general, they appear to have been due to introduction of *P. infestans* genotypes from outside Asia, most probably in seed tubers: the movement of seed tubers motivated by the desire to have virus-free potatoes provides a remarkably effective method of transporting strains of *P. infestans* into new locations (Fry, 2020). These genotypes had either been generated by sexual recombination in North America or Europe (from pathogen strains ultimately originating in Mexico) and then moved into Asia, or had possibly been introduced directly from Mexico, a centre of diversity and possible origin of the pathogen.

In the late 1980s, as these populations shifts were getting underway, metalaxyl, the first fully systemic fungicide for control of oomycete pathogens, was introduced for the control of late blight in parts of Asia. Metalaxyl-resistant strains of *P. infestans* appeared shortly

thereafter in Korea, India, Japan, and China. In Japan, Korea, and China, metalaxyl resistance was found only in isolates of new genotypes and not in those belonging to the US-1 lineage (Gotoh et al., 2005; Nishimura et al., 1999); it is not clear if selection occurred within the new migrant genotypes or if genotypes that were already metalaxyl-resistant were introduced to Asia. However, Akino et al. (2014) noted that the occurrence of the metalaxyl-resistant A2 genotype JP-1 was not always associated with use of metalaxyl; indeed, its appearance probably predated the commercial introduction of metalaxyl in Japan in 1988 (Kato et al., 1998), which implies that JP-1 was already metalaxyl-resistant when it arrived in Japan. In India, it is possible that selection for metalaxyl resistance also occurred within the preexisting US-1 population (which was in the process of being displaced), but this is implied only by the study of Chimote et al. (2010) and not by other studies of the Indian *P. infestans* population. The combination of the A2 mating type with the mtDNA haplotype Ib reported by Chimote et al. (2010) is, as noted above, very unusual; it has also been reported from the Netherlands (Li et al., 2012), but not elsewhere, necessitating a cautious approach to the interpretation of its significance.

In most of the potato-producing countries of Asia, the *P. infestans* population remains clonal and although both mating types have been found, evidence for sexual reproduction of the pathogen is limited to a few observations in Nepal and Japan. The occurrence of highly clonal populations despite the presence of both mating types is also typical of many European countries (e.g., the UK, Ireland) and of the USA (Fry, 2020).

The characteristics of these new populations of *P. infestans* are indicative of pathogen migrations from multiple sources. Thus, the A2 isolates, which were the first indicator of new populations in Asian countries, had diverse characteristics. For example, the A2 genotype JP-1 found in Japan, Korea, and Indonesia had the IIa mtDNA haplotype, whereas the A2 population found in Thailand, China, and Nepal during 1994 to 1997 possessed the Ia haplotype. Similarly, the new A1 populations also differed in mtDNA haplotypes (Ia, IIa, IIb) and other characteristics such as allozyme genotype, RG57 fingerprint, and SSR genotype (Figure 2c). Genotyping results also suggest that China experienced multiple introductions of *P. infestans* from Europe, Russia, the USA, and South America (Guo et al., 2010).

Some clonal lineages were clearly present across several Asian countries (Figure 2), but establishing the identity and patterns of spread of these lineages in time and space has been challenging: even comparing results obtained by different research groups within the same country may be difficult. This is because of the lack of consensus on the naming of *P. infestans* genotypes and on standard methods for determining them. Forbes et al. (1998) described a global marker database for *P. infestans* based on RFLP (RG57) fingerprint, mating type, allozyme genotype, mtDNA haplotype, metalaxyl sensitivity, and virulence, with a standard system (a two-letter country code and a unique number) for naming MLGs. However, this system was not universally adopted, nor did researchers necessarily check when naming a genotype in a new location if it had previously been reported and named elsewhere. As a result, the same lineage may appear in different countries, or even within the same country, under different names (Table 1). The advent of SSR genotyping and the subsequent abandonment of RG57 fingerprinting have further complicated the issue of defining and naming genotypes (particularly well exemplified by the published papers on *P. infestans* genotypes in China and in Korea, described above). Reconciling published genotype names is challenging, requiring levels of international cooperation proposed within the AsiaBlight network; without such an effort, routes of pathogen migration cannot be elucidated.

Thus JP-1 has been found in Japan, Korea, and Indonesia, but the route of its spread is unclear. The A1 SIB-1/JP-2 genotype is one of the most widespread genotypes. It has been found in continental China, Far-Eastern and European Russia, Poland, and Thailand as well as Japan, and has similarities to genotypes reported from continental Europe, the UK, and Ireland. On the basis of these comparisons, Akino et al. (2010) suggested that JP-2 (SIB-1) originated in Europe, but, after its introduction to Japan, mutation resulted in differences in some SSR alleles between it and the similar Northern Ireland genotype NI-1 (which equates to the SSR genotype EU_8_A1). Genotypes belonging to the A1 US-11 clonal lineage are also found in several Asian countries. There is strong circumstantial evidence that the US-11 genotypes of *P. infestans* that displaced the US-1 population in Taiwan in 1998–1999 were introduced directly from the USA (Deahl et al., 2002). However, US-11 types have also been found recently in South Korea and Vietnam and it is unclear how this clonal lineage reached these countries.

Most strikingly, the European 13_A2/Blue 13 clonal lineage was discovered to be present in Asia very soon after its first European findings in isolates collected in 2004 in the Netherlands and Germany (Cooke et al., 2012); preliminary results from the AsiaBlight coarse-scale mapping project indicate that the 13_A2 clonal lineage is now very widespread across mainland Asia (Cooke et al., 2017). How it arrived in Asia and how it subsequently spread is unclear but may be elucidated by further comparative population studies. The earliest finding of 13_A2 in Asia reported to date was an isolate collected in 2005 in Yunnan, China (Li et al., 2013b). It was then identified in India in isolates collected in 2009 (Chowdappa et al., 2013) as well as subsequently in 2014 (Dey et al., 2018) and is now known to be also present in Nepal (Adhikari, 2017), Bangladesh (Islam et al., 2020; Kessel et al., 2017), Pakistan (Raza et al., 2020), and Myanmar (D. E. L. Cooke, unpublished data). A high level of subclonal diversity has been reported in the 13_A2 lineage in Asia both from China (Li et al., 2013b) and India where some unique subclonal variants were identified (Dey et al., 2018), as well as recently from Bangladesh (M. R. Islam, Bangladesh Agricultural University, Bangladesh, 2020, personal communication). In contrast, in Pakistan all 13_A2 samples from 2019–2020 that were successfully genotyped belonged to a single subclonal variant, suggesting a single recent introduction of this genotype (Raza et al., 2020; Figure 2d).

Recently, Wang et al. (2020) reported a lack of gene flow between the *P. infestans* populations in China and India, but the significance of their findings is difficult to interpret as it appears that the populations compared belonged to different clonal lineages

and mating types. A lack of direct gene flow is not unexpected in view of the natural Himalayan barrier, restricted trade in agricultural commodities, and strict border surveillance between these countries. Broadly speaking, while physical barriers such as the Himalayas or the sea may result in locally distinct populations, political borders between countries present little barrier to the movement of *P. infestans* genotypes. Indeed, windborne movement of *P. infestans* sporangia between contiguous regions allows spread of introduced and selected genotypes as is suspected in eastern India from Bangladesh and Nepal (Dey et al., 2018). Thompson et al. (2016) noted the need for management of invading pathogens to be informed by epidemiology rather than administrative boundaries. Asian populations of *P. infestans* clearly illustrate the lack of effectiveness of political barriers in limiting spread of aggressive, sometimes fungicide-resistant pathogen genotypes, and exemplify the need for international cooperation through networks such as AsiaBlight to reduce the impact of epidemic late blight on food production (Carvajal-Yepes et al., 2019).

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CONFLICT OF INTERESTS

The authors further state there are no conflict of interests.

DATA AVAILABILITY STATEMENT

Data sharing not applicable to this article as no data sets were generated during the current study.

ORCID

Sanjoy Guha Roy https://orcid.org/0000-0002-6159-846X
David E. L. Cooke https://orcid.org/0000-0002-9154-7954
Louise R. Cooke https://orcid.org/0000-0002-2761-3689

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