A Global Marker Database for *Phytophthora infestans*

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ABSTRACT

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A marker database was compiled for isolates of the potato and tomato late blight pathogen, *Phytophthora infestans*, originating from 41 locations which include 31 countries plus 10 regions within Mexico. Presently, the database contains information on 1,776 isolates for one or more of the following markers: restriction fragment length polymorphism (RFLP) "fingerprint" consisting of 23 bands; mating type; dilocus allozyme genotype; mitochondrial DNA haplotype; sensitivity to the fungicide metalaxyl; and virulence. In the database, 305 entries have unique RFLP fingerprints and 258 entries have unique multilocus genotypes based on RFLP fingerprint, dilocus allozyme genotype, and mating type. A nomenclature is described for naming multilocus genotypes based on the International Organization for Standardization (ISO) two-letter country code and a unique number. Forty-two previously published multilocus genotypes are represented in the database with references to publications. As a result of compilation of the database, seven new genotypes were identified and named. Cluster analysis of genotypes from clonally propagated populations worldwide generally confirmed a previously published classification of "old" and "new" genotypes. Genotypes from geographically distant countries were frequently clustered, and several old and new genotypes were found in two or more distant countries. The cluster analysis also demonstrated that A2 genotypes from Argentina differed from all others. The database is available via the Internet, and thus can serve as a resource for *Phytophthora* workers worldwide.

Additional keywords: DNA fingerprints, population genetics, RG57

The development of molecular markers stimulated new insights into the genetic structure of plant pathogen populations (13,17,19,23,24,32). Several markers, including the moderately repetitive nuclear restriction fragment length polymorphism (RFLP) probe RG57, have been particularly useful in population analysis of the potato and tomato late blight pathogen *Phytophthora infestans* (Mont.) deBary (9,15,17,19,26–28). Knowledge of pathogen population structure has been used to develop or modify disease management strategies (21,25) and in deployment of host resistance (22). Population studies on *P. infestans* also stimulated new hypotheses about historical migrations and the genetic structure of the global pathogen population (11). This information may be useful for interpreting changes in overall disease severity. For example, recent changes in the population structure of *P. infestans* have been linked with increased difficulty in the management of late blight in North America and Europe (8).

To date, most studies on *P. infestans* populations concerned North America and Europe (11) and produced detailed information on the pathogen populations in these areas. In contrast, little is known of the pathogen population structure in South America, Africa, and parts of Asia. As a result, many questions regarding the global population structure of this important plant pathogen remain unanswered (11).

For example, analysis of isolates from several countries for mating type, allozyme genotype, and DNA fingerprint led to the hypothesis that a single clonal lineage, US-

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Table 1. Description of variables in the *Phytophthora infestans* global database

Variable	Variable description
Isolate identification	
CORNELL	Cornell isolate code
ISOLATE	Original isolate designation of contributing institution
COUNTRY	Country where isolated
ISO	International Organization for Standardization two-letter country code
LOCATION	Region of country where isolated
HOST	Potato, tomato, etc.
CULTIVAR	Cultivar of host
DATE	Date or year isolated
COMMENT	Information not covered in the above variables
Markers	
MATING_T	Mating type ('A1', 'A2', or 'SF')
GPI	*Glucose-6-phosphate isomerase* (*Gpi*) genotype
PEP	*Peptidase* (*Pep*) genotype
FING_PRT	DNA fingerprint[a]
FP9A	DNA fingerprint band between bands 9 and 10 [b]
FP14A	DNA fingerprint band between bands 14 and 15 [b]
FP24A	DNA fingerprint band between bands 24 and 25 [b]
FP25A	DNA fingerprint band after band 25 [b]
MT_DNA	Mitochondrial DNA pattern[c]
METALAX	Sensitivity to metalaxyl ('R', 'M', 'S') [d]
VIRULENCE	Specific virulence on 11 known *Solanum demissium* R-genes
Summary	
GENOTYPE	Multilocus genotype name
PUB_GEN	Published genotype name which is inconsistent with nomenclature [e]
SOURCE	Original supplier of isolate, infected tissue or data
REFERENCE	Where published initially

[a] As determined with the moderately repetitive DNA probe RG57 (15).
[b] These are additional DNA fingerprint bands discovered after bands 1 to 25 were numbered.
[c] As described by Goodwin (10) or Carter et al (3).
[d] R = resistant, M = moderately resistant and S = sensitive, as described by Therrien et al. (29).
[e] Based on nomenclature described in Materials and Methods.

1, dominated most populations of *P. infestans* outside Mexico until recently (13). The universality of US-1 was clearly demonstrated with marker analyses (13), but its origin has been disputed (1). One interpretation of the data is that US-1 was introduced into the United States in the 1840s and subsequently to Europe, where it caused the devastating epidemics which were primary factors leading to the Irish Potato Famine (13). An alternative interpretation suggests that US-1 was introduced into Europe and the United States from South America, where it had existed during pre-colonial times (1).

Answering this and other questions regarding the global population structure of *P. infestans* will depend, at least in part, on the availability of marker information from different parts of the world. One important step toward making this information available would be agreement on a nomenclature for genotype designations, standardization of genetic data, both in terms of markers used and the way data are stored, and compilation of marker data into one database which is readily available to all researchers.

The purpose of this paper is to propose standardization of *P. infestans* nomenclature and marker data, and compile a large amount of existing marker data into a single database, which will be available over the Internet. We also demonstrate how the database can be used to examine the relationship among genotypes from clonally propagated populations (clonal lineages). This analysis supports some earlier hypotheses and provides new information on the relatedness of genotypes in South America. This database should form a solid basis for future studies on the genetic structure of populations of *P. infestans.*

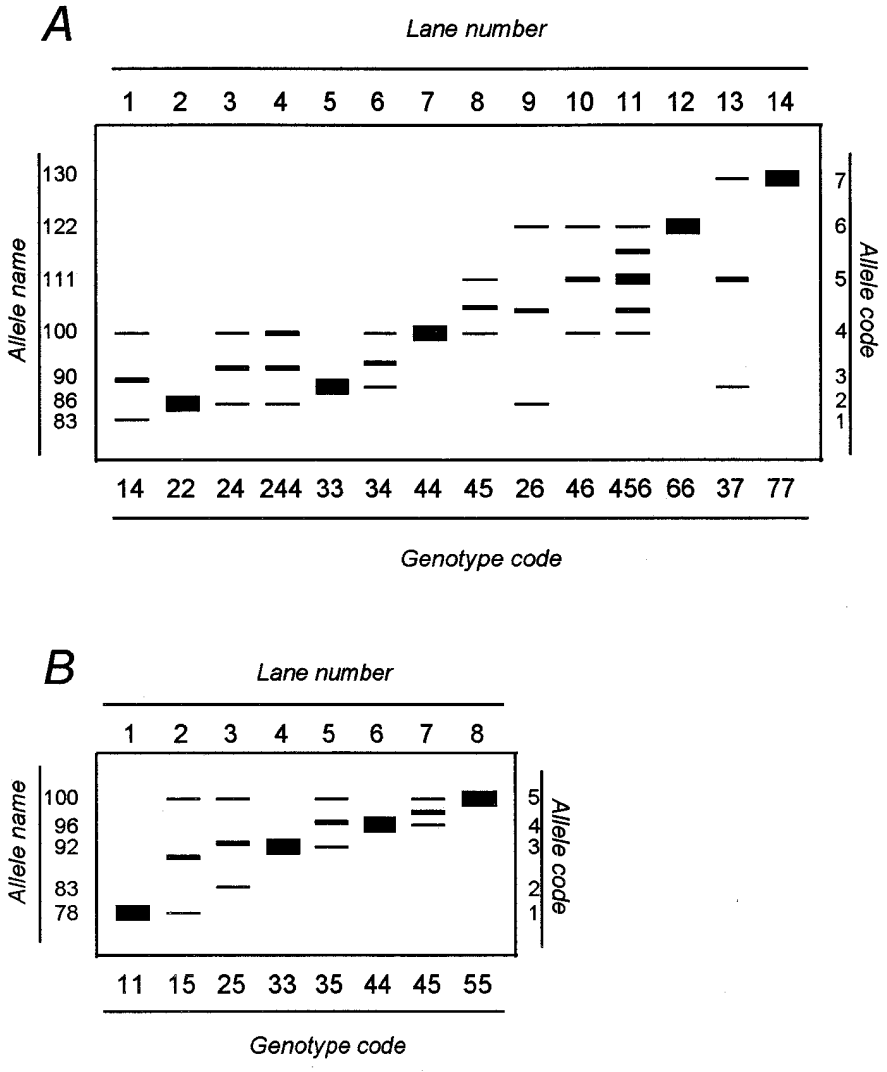

Fig. 1. Deciphering the allozyme genotypes of *Phytophthora infestans*: the Rosetta Stone. The most commonly detected genotypes worldwide are shown for **(A)** the *Glucose-6-phosphate isomerase* (*Gpi*) locus and **(B)** the *Peptidase* (*Pep*) locus. Both enzymes are dimeric, giving three bands for each heterozygous genotype: two homodimer bands and one heterodimer band. Homozygous genotypes have a single band. Genotypes are drawn approximately to scale assuming a migration distance of 5 cm for the *100/100* homodimer band at each locus. Allele names on the left indicate the approximate migration distance of each homodimer band. The coding for each allele is on the right. Allele codes are combined to form the genotype codes indicated at the bottom of each lane. The 14 lanes at the *Gpi* locus correspond to the following genotypes: lane 1, *83/100*; lane 2, *86/86*; lane 3, *86/100*; lane 4, *86/100/100*; lane 5, *90/90*; lane 6, *90/100*; lane 7, *100/100*; lane 8, *100/111*; lane 9, *86/122*; lane 10, *100/122*; lane 11, *100/111/122*; lane 12, *122/122*; lane 13, *90/130*; lane 14, *130/130*. The eight lanes at the *Pep* locus correspond to the following genotypes: lane 1, *78/78*; lane 2, *78/100*; lane 3, *83/100*; lane 4, *92/92*; lane 5, *92/100*; lane 6, *96/96*; lane 7, *96/100*; lane 8, *100/100*. Notice the two genotypes at the *Gpi* locus with three alleles: *Gpi 86/100/100* (lane 4) and *Gpi 100/111/122* (lane 11). The Gpi *86/100/100* genotype gives an "unbalanced" heterozygote pattern with an approximately 1:4:4 ratio of intensities for bands representing the *86/86* homodimer, *86/100* heterodimer, and *100/100* homodimer bands, respectively. Compare this to the "balanced" *86/100* heterozygote pattern in lane 3. The *100/111/122* genotype has five bands in an approximately 1:2:3:2:1 ratio of intensities (16). This is due to co-migration of the *111/111* homodimer and *100/122* heterodimer bands. A possible additional allele has been found at the *Pep* locus (13). This allele was found in isolates from Costa Rica and has a migration distance of approximately 94% compared to the *100* allele between the *Pep 92* and *96* alleles. However, this allele has not been confirmed by analyses with proper controls so was not included in the figure. It was coded *Pep* allele 6 in the database. This figure was meant to show typical idealized separation distances among the bands on a gel; actual distances between bands may vary due to the composition of the gel and pH of the buffers used.

MATERIALS AND METHODS

Database. The database contains marker data from several published (4–6,9,12–14,17–20,28) and unpublished studies (S. B. Goodwin and G. A. Forbes, *unpublished*). Isolate characteristics were entered into the database using 24 categories (Table 1). Eight identification variables contain typical passport data related to isolate history and maintenance. Unusual observations can be recorded in a variable for comments. There are 11 categories of marker data: mating type; dilocus allozyme genotype at the two loci *glucose-6-phosphate isomerase (Gpi*) and *peptidase* (*Pep*); genomic DNA fingerprint as determined with probe RG57, including four separate variables for rare DNA fingerprint bands; mitochondrial DNA haplotype; sensitivity to the fungicide metalaxyl; and specific virulence. Data for allozyme genotypes and DNA fingerprints were coded as indicated in Figures 1 and 2, respectively. The final four categories contain summary information. One category indicates the multilocus genotype designation of each isolate, determined by analysis of the 23 RFLP fingerprint loci, dilocus allozyme genotype, and mating type. One variable retains previously published genotype designations which do not adhere to the nomenclature outlined in this paper. One category indicates the original source of the isolates or data, and the final category indicates the reference in which the data were published initially.

The database is easily expandable to accommodate additional markers that may

prove useful in the future. The isolates were collected at different times and do not necessarily reflect the current populations of the countries in which they were collected. Some isolates listed in the database are currently available in a culture collection curated by W. E. Fry (Cornell University); however, many isolates are no longer available.

Comparison of genotypes from asexual populations. For countries where sexual reproduction has not been demonstrated, or demonstrated only very recently (all except Mexico, Poland, and the Netherlands), the units of analysis were the multilocus genotypes described above, which were constructed for each isolate and based on 23 RFLP fingerprint bands, mating type, and genotype at the *Gpi* and *Pep* allozyme loci. RFLP band 4, which has been scored inconsistently, and band 25, which occurred in all fingerprints, were excluded from analyses.

Each RFLP band was treated as one dichotomous variable, with values of 0 or 1 for absence and presence, respectively. Data for allozyme genotypes were converted to binary format by creating a dichotomous variable with values of 0 or 1 (absence or presence) for each known allele (seven for *Gpi* and six for *Pep*). Similarity of multilocus genotypes in asexual populations was estimated with the Jaccard coefficient (31), which was then subtracted from unity to represent genetic distance. Trees were constructed from the distance matrix using the unweighted pair-group method of averages (UPGMA) algorithm. All analyses were done using SAS (release 6.12, SAS Institute, Inc., Cary, NC).

RESULTS

At present, the database contains information on isolates from 41 locations, including 31 countries plus 10 regions within Mexico (Table 2). There are 1,776 entries, of which 1,227 have RFLP fingerprints, based on a minimum common set of 23 bands. Overall, 369 RFLP fingerprints are unique within their respective sites (Table 2), although some of these occur in more than one site. There are 305 unique RFLP fingerprints in the entire database. Among 976 isolates with complete data for RFLP fingerprint, dilocus allozyme genotype, and mating type, there are 288 multilocus genotypes which are unique within their respective site (Table 2), and 258 which are unique in the database. The number of unique multilocus genotypes is smaller than the number of unique RFLP fingerprints because some entries which have RFLP data do not have allozyme data. Most of the unique multilocus genotypes come from Mexico, the Netherlands, and Poland, where sexual recombination is known to occur (4,28,30). There is also a large number of unique genotypes from the United States and Canada, for which there is evidence of repeated introductions of

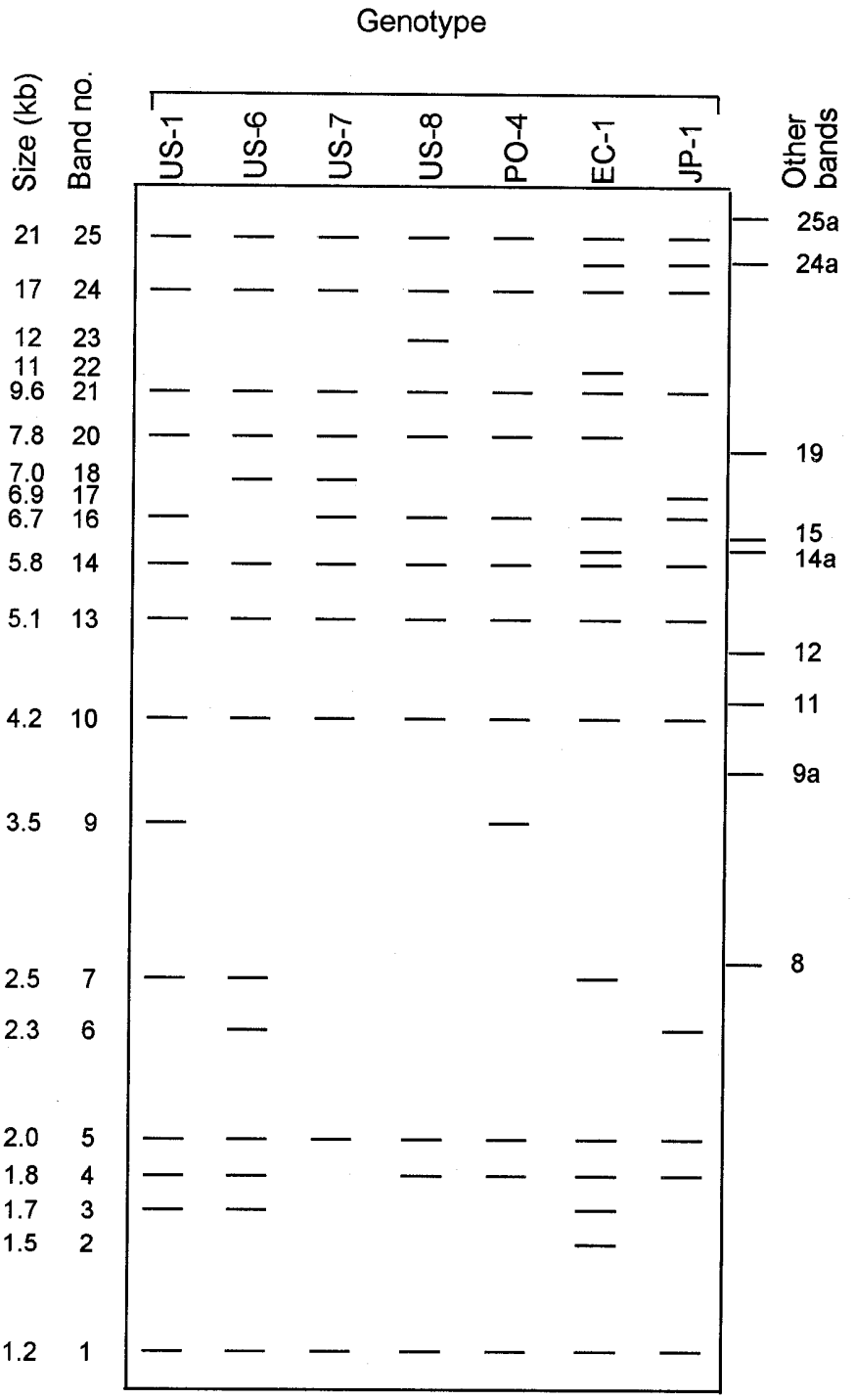

Fig. 2. Coding of DNA fingerprint genotypes of *Phytophthora infestans* for the global database. Fingerprint patterns are as generated using the moderately repetitive probe RG57 as described elsewhere (15). Each band represents a different genetic locus that segregates for the presence or absence of a band (15). Approximate band positions are indicated for all seven genotypes that occurred 10 or more times in the global database. Each genotype was the most commonly detected clone in the following locations: US-1, worldwide (11,13); US-6, US-7, and US-8, the United States and Canada (12,17); PO-4, eastern Europe (28); EC-1, northern South America (5,25); and JP-1, east Asia (20). The major bands in each genotype (in bold) and their approximate sizes in kilobases are indicated on the left. The approximate positions of bands not present in these genotypes or that are rare are indicated by the arrows on the right. For the database, fingerprint genotypes were coded where 0 = absence and 1 = presence of a band at each fingerprint locus. Some investigators scored presence with 1 for a probable heterozygote and 2 for a probable homozygote; both types of scoring are present in the database and were scored as 1 for the analyses. By tilting the figure 90 degrees clockwise, the genotypes can be read from left to right like a bar code. The location of band 4 was indicated to be consistent with previous publications. However, this band is not always repeatable and seems to depend on the particular batch of probe used. Therefore, variation at fingerprint locus 4 is difficult to interpret and should be excluded from all analyses. This schematic is drawn to scale from a real gel but is intended for illustration only; actual migration distances will vary depending on the gel conditions used.

new genotypes from Mexico (12,17,19), and recent evidence for probable sexual reproduction (17). The US-1 genotype was found in 20 countries worldwide (Table 2).

Nomenclature. We propose the use of multilocus genotype designations, consisting of the internationally accepted, two-letter code from the International Organization for Standardization (ISO) for the country where the genotype was isolated and a unique number. This system is in agreement with an earlier genotype designation for US-1 by Goodwin et al. (13) using the same markers. Once a genotype has been identified, its designation is used wherever it is subsequently found. For example, US-1 was originally identified in the United States, but it has subsequently been found in many countries where it retains the US-1 designation (13). A few previously published genotype names are not consistent with this nomenclature (12,17). These genotypes were given new names consistent with the nomenclature; the old names have been maintained in the database as a separate variable.

An extension of the nomenclature described above was adopted by Goodwin et al. (12) to identify genotypes which have arisen from within a single clonal lineage. These genotypes are identical to other members of the same clonal lineage except for changes at one, or at most two, allozyme or DNA fingerprint loci. They are identified by placing a decimal point and a number after the genotype name. For example, US-1.1 and US-1.2 are variants within the US-1 lineage, while US-6.1 is a genotype which has developed within the US-6 lineage.

Currently, the database contains 42 multilocus genotypes which were published previously (Table 3).

An additional seven previously unnamed genotypes were identified after compilation of this database (Table 4). These were given designations based on the country where the genotypes were found and a unique number as described above.

Comparison of multilocus genotypes. Clustering of multilocus genotypes from clonally propagated populations generally corroborated the classification of "old" and "new" genotypes proposed by Spielman et al (27). One large cluster was formed by

Table 2. Summary statistics and frequencies of restriction fragment length polymorphism (RFLP) and multilocus genotypes found in sites represented in the global marker database for *Phytophthora infestans*

			Genotypes		Mating type		
Country or region[a]	**ISO code[b]**	**Entries[c]**	**RFLP[d]**	**ML[e]**	**A1**	**A2**	**SF[f]**
Argentina	AR	15	2	5	0	15	0
Australia	AU	5	2	2	5	0	0
Byelorussia	BY	7	1	1	7	0	0
Bolivia	BO	1	1	1	0	1	0
Brazil**	BR	7	2	4	4	3	0
Canada**	CA	75	13	12	66	8	0
China**	CN	6	1	1	6	0	0
Colombia**	CO	12	2	2	12	0	0
Costa Rica	CR	9	1	1	8	0	0
Ecuador**	EC	74	2	2	74	0	0
Estonia	EE	2	1	2	1	0	0
France	FR	14	8	1	14	0	0
Germany**	DE	16	2	0	16	0	0
Guatemala	GT	1	0	0	0	1	0
Ireland**	IE	2	1	1	2	0	0
Israel	IL	9	1	1	0	9	0
Italy**	IT	1	1	0	1	0	0
Japan**	JP	30	2	2	15	15	0
Korea**	KR	56	2	2	1	55	0
Mexico	MX						
Central Mexico		6	5	5	2	4	0
Chapingo		9	6	6	5	4	0
Chiapas		11	3	6	11	0	0
Los Mochis		88	3	4	63	25	0
Michoacan		10	3	3	7	3	0
Nuevo Leon		4	1	1	4	0	0
Puebla		26	11	1	15	11	0
Saltillo		41	13	1	13	27	1
Toluca		111	55	63	63	43	0
Vera Cruz		12	2	3	11	1	0
Netherlands**	NL	211	131	11	107	99	2
Peru**	PE	45	4	4	45	0	0
Philippines**	PH	28	1	2	28	0	0
Poland**	PL	251	62	81	189	42	5
Romania	RO	1	0	0	0	1	0
Russia**	RU	7	2	3	3	4	1
Rwanda**	RW	21	3	4	21	0	0
Spain	ES	2	1	1	2	0	0
Switzerland**	CH	3	1	1	3	0	0
Taiwan**	TW	3	1	1	3	0	0
United Kingdom**	GB	16	4	2	15	1	0
United States**	US	528	12	16	276	236	0
Total		1,776	369	288	1,118	608	9

[a] Locations indicated with ** have the US-1 genotype.
[b] International Organization for Standardization, Alpha 2 code.
[c] Number of isolates.
[d] Number of RFLP fingerprints which are unique within each site. Genotypes based on 23 RFLP bands.
[e] Number of multilocus genotypes within each site. Genotypes based on 23 RFLP bands, dilocus allozyme genotype, and mating type.
[f] Self fertile.

Table 3. Previously published multilocus genotypes[a] which are currently represented in the database

Genotype	Mating type	*Gpi*[b]	*Pep*[c]	RFLP fingerprint[d]	Source
AU-1	A1	24	55	1001100001001101010110011	(13)
AU-2	A1	24	55	1011101000001100000110011	(13)
BR-1	A2	44	55	1011101000001100001111011	(13)
CA-1	A1	24	35	1111101011001101001110011	(12)
CA-2	A1	44	55	1011001000001100001110011	(12)
CA-2.1	A1	44	55	1011001000001100001111011	(12)
CA-3	A2	24	55	1111101001001001100110011	(12)
CA-4	A2	45	55	1001000001001101000110011	(17)
CA-5	A2	44	55	1000110000001101000110011	(17)
CA-6	A2	44	55	1010001001001100010110011	(17)
CA-7	A2	44	55	1001000000001100010110011	(17)
CR-1	A1	44	56	1001000001001101000110011	(14)
EC-1	A1	34	45	1111101001001101000111011	(5)
EE-1	A1	34	55	1001100001001100100110011	(17)
EE-2	SF	34	55	1010101011001101000110011	(14)
IL-1	A2	44	55	1001100001001101000110011	(13)
JP-1	A2	44	44	1001110000001101100010011	(18)
RU-1	A1	44	55	1011101011001101000110011	(14)
RW-1	A1	34	25	1111111011001101001111011	(13)
RW-2	A1	34	55	1111101001001101001111011	(13)
US-1	A1	24	35	1011101011001101000110011	(13)
US-1.1	A1	24	55	1011101011001101000110011	(28)
US-1.2	A1	24	35	1011101010001101000110011	(13)
US-1.3	A1	24	35	1011101001001101000110011	(13)
US-1.4	A1	24	55	1011101010001101000110011	(12)
US-1.5	A1	24	35	1011101011001101010110011	(17)
US-1.6	A1	24	35	1011101011001101000111011	(14)
US-1.7	A1	44	35	1011101011001101000110011	(14)
US-2	A1	24	35	1011101001001101011110011	(12)
US-3	A1	24	35	1011100000001101000110011	(12)
US-4	A1	44	33	1011101001001101100110011	(12)
US-5	A1	44	35	1011101001001101011110011	(12)
US-6	A1	44	35	1011111001001100010110011	(17)
US-6.1	A1	44	33	1011111001001100010110011	(12)
US-6.2	A1	44	35	1011101001001100010110011	(12)
US-6.3	A1	44	35	1011111001011100010110011	(12)
US-6.4	A1	44	55	1011011001001100010110011	(12)
US-6.5	A1	44	35	1011111001001100010010011	(12)
US-7	A2	45	55	1011101011001101000110011	(17)
US-8	44	A2	456	1001100001001101000110111	(17)
US-9[e]	A1	44	25	…	(17)
US-10[e]	A2	56	55	…	(17)

[a] Genotypes based on 23 restriction fragment length polymorphism (RFLP) bands, dilocus allozyme genotype, and mating type. New names exist in the database for certain genotypes which do not concur with the proposed nomenclature (for example, Canadian genotype CDA-1 has been changed to CA-1). Originally published names have been retained in the database to facilitate cross referencing. Allozyme genotypes and DNA fingerprints are coded as indicated in Figs. 1 and 2, respectively.

[b] *Glucose-6-phosphate isomerase.* Alleles at the *Gpi* locus are coded as 86 = 2, 90 = 3, 100 = 4, 111 = 5, and 122 = 6.

[c] *Peptidase.* Alleles at the *Pep* locus are coded as 83 = 2, 92 = 3, 96 = 4, and 100 = 5.

[d] DNA fingerprint bands revealed by the moderately repetitive probe RG57 (15) Presence and absence of bands are indicated by 1 and 0, respectively. Bands 1 to 25 are listed from left to right. Bands 4 and 25 were not used in analyses.

[e] US-9 and 10 are based on novel *Gpi* and *Pep* patterns. RFLP fingerprints are not known.

Table 4. Multilocus genotypes[a] named as a result of compilation of the database

Genotype	Mating type	*Gpi*[b]	*Pep*[c]	RFLP fingerprint[d]
AR-1	A2	44	34	1001000000000000000111111
AR-2	A2	44	44	1001000000000000000111111
AR-3	A2	44	34	1001100010000000000101111
AR-4	A2	44	44	1001100010000000000101111
AR-5	A2	44	45	1001100010000000000101111
FR-1	A1	44	25	1010111111001101001110101
ES-1	A1	34	55	1100100001001101000110011

[a] Genotypes based on 23 restriction fragment length polymorphism (RFLP) bands, dilocus allozyme genotype, and mating type.

[b] *Glucose-6-phosphate isomerase.* Alleles at the *Gpi* locus are coded as 90 = 3 and 100 = 4.

[c] *Peptidase.* Alleles at the *Pep* locus are coded as 83 = 2, 92 = 3, 96 = 4 and 100 = 5.

[d] DNA fingerprint bands revealed by the moderately repetitive probe RG57 (15). Presence and absence of bands are indicated by 1 and 0, respectively. Bands 1 to 25 are listed from left to right. Bands 4 and 25 were not used in analyses.

old genotypes which belong to the US-1 lineage (Fig. 3). Old genotypes from the United States and Canada which do not belong to the US-1 lineage clustered together and adjacent to the US-1 lineage cluster. One previously described genotype from Russia (RU-1) clustered among the US-1 lineage genotypes and may belong to that lineage. The classification system of Spielman et al. (27) originally was based on mating type and dilocus allozyme genotype. This analysis confirms that it is also generally valid after examination of a more complex multilocus genotype including RFLP fingerprints.

New genotypes generally clustered according to mating type. Genotype CA-3 from Canada was an exception, because it was not closely associated with any other A2 genotypes (Fig. 3).

The cluster analyses indicated some degree of geographical structuring (genotypes from Argentina, and some from Canada and the United States, were closely clustered), but there was also clustering of genotypes from distant countries. One genotype from Rwanda was most closely associated with EC-1 from the Andean region. BR-1 from Brazil and Bolivia (13) was most closely associated with genotypes CA-2.1 and CA-2 from Canada. In addition to showing other close associations among genotypes from geographically distant sites, the cluster analysis indicated that genotype PO-57, first named in Poland but also found in Russia, is identical to IL-1 from Israel.

Compilation of the database also demonstrated that several genotypes are distributed internationally (Table 5). In some cases, the same genotype has been found in neighboring countries. For example, EC-1 is found in Colombia and Ecuador, JP-1 in Japan and South Korea, US-6 in Canada and the United States. Some genotypes, however, are globally distributed. The global distribution of US-1 was demonstrated previously (13) and the genotype is shown here to occur in 20 countries (Table 2). Genotypes thought to have developed within the US-1 lineage (US-1.1, US-1.2, US-1.3) also occur on several continents (Table 5). It is not possible to tell from this analysis whether the global distribution of these genotypes is a result of migration or whether they have developed independently from the US-1 genotype within each site.

The cluster analysis of asexual populations sheds new light on the genetic structure of the population of *P. infestans* in South America. The A2 mating type had been reported for Brazil (2), Bolivia (13), and Argentina (7), but nothing was known of the relatedness of these populations. Here it is shown that the A2 isolates from both Brazil and Bolivia are the same genotype, BR-1. The A2 genotypes from Argentina are related among themselves but distinct from BR-1. The small number

of samples represented in the database from each of these countries (Table 2) makes it impossible to comment on the presence of other genotypes in this region. US-1 also occurs in Brazil (13), but to date it has only been found on tomato (2). The EC-1 lineage which was recently described in Ecuador (5) is seen here to extend north to Colombia. The US-1 lineage also occurs in these countries and Peru (Table 2).

DISCUSSION

The database compiled here is an important tool for studying the global population structure of *P. infestans*. It will be of utility to researchers who wish to examine global population patterns or compare local genotypes with a large international collection. The cluster analysis is one example of how this database can be used for assessing the relatedness among genotypes from clonal populations.

Most of the genetic diversity represented in the database is associated with North America and Europe (Table 2). In part, this reflects the global population structure of the pathogen. The presence of both mating types, and associated sexual recombination, in Mexico and Europe certainly has contributed to the large number of genotypes which have been found in those areas. Nonetheless, the information in the database also reflects a geographic imbalance in research activity, because very little sampling and marker analyses have been done outside North America, Europe, and a few locations in Asia. More information on the *P. infestans* populations in Africa, South America, and Asia could assist researchers in the development of improved disease management strategies. Information gained from pathogen population studies in the past has led to recommendations for refinement or modification of disease management approaches (21,25). Knowledge of pathogen population structure also can play a key role in selection and deployment of durable host resistance (22).

The resurgence of late blight in North America and increased severity in Europe (8) has heightened interest among researchers. Genetic characterization of *P. infestans* isolates undoubtedly will be conducted by an increasing number of laboratories. Agreement on nomenclature and data storage structure will greatly facilitate comparative studies. Failure to agree on nomenclature will probably lead to confusion, reduced complementarity, and even unnecessary replication of research activities.

The nomenclature explicitly proposed here is based on earlier genotype designations (13). It is simple, yet provides for an unambiguous identification of genotypes. Incorporation of existing and future marker data into one database will help ensure standardization of data format as well as

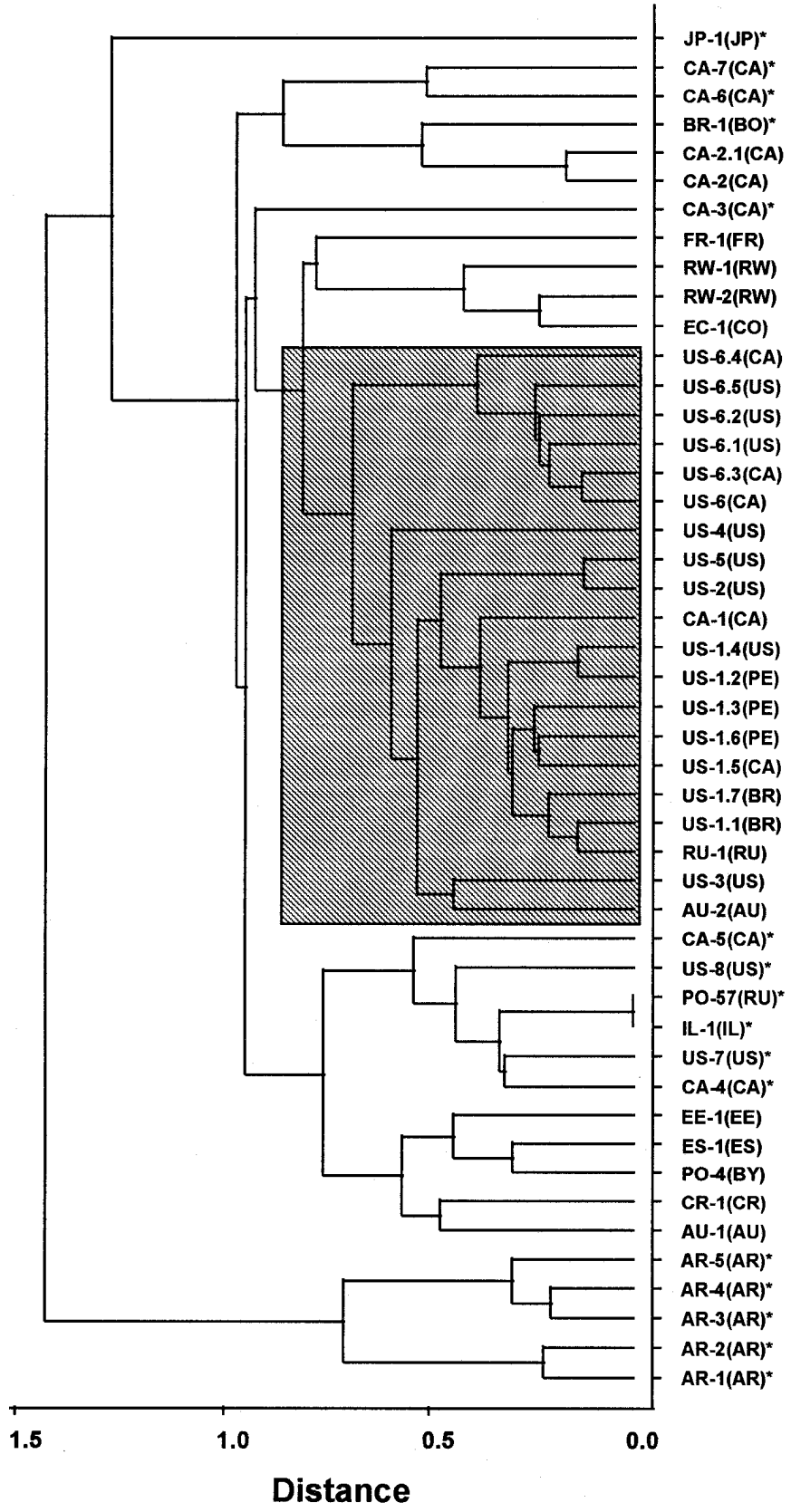

Fig. 3. Cluster analysis of asexual genotypes of *Phytophthora infestans* based on a distance coefficient (Jaccard) for multilocus genotypes consisting of restriction fragment length polymorphism fingerprint, mating type, and dilocus allozyme genotype. Genotype labels are the International Organization for Standardization (ISO) two-letter country code plus a unique number (see Table 2). ISO codes in parentheses indicate country where genotypes were found. Shaded area identifies "old" genotypes (27). Asterisks indicate A2 genotypes. Vertical lines indicate absolute ties where two or more isolates have the same genotype.

nomenclature. One limitation to this system is that it is directly linked to the markers used to define genotypes. Addition of new marker information may differentiate among isolates which now have the same genotype designation. This problem should be addressed by those utilizing new marker technologies.

The utility of this database was demonstrated with one cluster analysis (Fig. 3). Even though this analysis was intended as an example, it generally confirmed the previously published classification of old and new genotypes and led to new observations regarding the global population structure of *P. infestans*. For example, one relevant statement can be made concerning management of the disease in South America. To date, only A2 genotypes have been found in association with potato production in Bolivia and only A1 genotypes have been found in association with potato production in Peru. Potato production is continuous across the border between Peru and Bolivia, and potato seed is traded between the two countries (J. Landeo, *personal communication*). Therefore, the potato production zones near the border between Peru and Bolivia represent an area were the A1 and A2 mating types could come in contact, perhaps for the first time, in the center of origin of potato. The increased genetic diversity resulting from sexual recombination and the epidemiological consequences of oospores may create new disease management problems for farmers in this important potato-growing region. Researchers should also be aware of new threats that increased pathogenic fitness of this pathogen may pose for wild tuber-bearing solanaceous species in the Andes, an important natural resource for the future.

Table 5. Multilocus genotypes from asexual populations represented by more than one country in the database

Genotype	Country
Old genotypes	
RU-1	Russia
	Rwanda
US-1.1	Brazil
	Canada
	Philippines
	United States
US-1.2	Peru
	United Kingdom
	United States
US-1.3	Peru
	United States
New genotypes	
BR-1	Bolivia
	Brazil
JP-1	Japan
	Korea
PO-4	Poland
	Byelorussia
PO-57	Poland
	Israel
	Russia
EC-1	Ecuador
	Colombia

Database availability. The database is available over the Internet via the Microbial Germplasm Database maintained at Oregon State University. To ensure that data standardization is maintained, we propose that anyone wishing to contribute new information first contact the corresponding author.

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