Implications of Sexual Reproduction for *Phytophthora infestans* in the United States: Generation of an Aggressive Lineage

P. D. Gavino, DuPont Fellow, Department of Plant Pathology, Cornell University, Ithaca, NY; **C. D. Smart** and **R. W. Sandrock**, Department of Plant Pathology, Cornell University, Ithaca, NY; **J. S. Miller**, Department of Plant Pathology, Washington State University, Pullman; **P. B. Hamm**, Department of Plant Pathology, P.O. Box 105, Oregon State University, Hermiston 97838; **T. Yun Lee**, Department of Plant Pathology, Cornell University, Ithaca, NY; **R. M. Davis**, Department of Plant Pathology, University of California, Davis 95616; and **W. E. Fry**, Department of Plant Pathology, Cornell University, Ithaca, NY

ABSTRACT

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Phytophthora infestans isolates (n = 26) collected in the Columbia Basin of Oregon and Washington in 1993, which had been characterized previously for mating type, metalaxyl sensitivity, and alleles at the *glucose-6-phosphate isomerase* locus, were analyzed for nuclear restriction fragment length polymorphism (RFLP) bands detected by probe RG57 and mitochondrial haplotype. Analyses involving the larger set of markers indicated that this group of isolates satisfied expectations of a sexual progeny: they contained much greater genetic diversity than has been reported for most other epidemic populations of *P. infestans* in the United States and Canada (16 unique multilocus genotypes); both mating types were present in proximity; all possible combinations of alleles occurred at many pairs of polymorphic loci; and two distinct mitochondrial haplotypes were distributed among the isolates. An in vitro laboratory cross involving the putative parents (US-6 and US-7) as parental strains produced progeny with the same general characteristics as the field isolates. Among the field progeny were two genotypes, US-11 and US-16, that had been described previously but from subsequent and largely clonal collections. Isolates obtained from tomatoes (n = 40) and potatoes (n = 7) in 24 counties in California in 1998 were analyzed as described above, and all except one US-8 isolate from potatoes were of the US-11 clonal lineage, consistent with the hypothesis that the US-11 lineage is an especially fit clonal lineage that has survived over time and can dominate pathogen populations over a large area. We conclude that the 1993 Columbia Basin collection represents a sexual progeny that generated the US-11 lineage, and that this lineage is particularly fit when tomatoes are part of the agroecosystem.

The recent widespread occurrence of both A1 and A2 mating type strains of *Phytophthora infestans* in the United States and Canada (7,13,20) has increased the probability of sexual recombination in this pathogen in these countries. Typically, production of antheridia and oogonia is initiated primarily when two individuals of alternate mating type (A1 and A2) occur in close proximity (17,23). Prior to the 1990s, A2 mating types were absent or extremely

rare in the United States and Canada (4,9), so the occurrence of sexual recombination was highly unlikely. Two possibilities resulting from sexual recombination are feared by growers and scientists: that the oospores in the soil might become a source of inoculum for late blight epidemics, and that sexual recombination might generate new genotypes of *P. infestans* that are particularly aggressive (7).

However, even after the introduction of A2 mating type strains, the contribution of sexual reproduction to the genetic structure of *P. infestans* in the United States and Canada appeared minimal. Most populations in a single field have been monomorphic for mating type (13,14,20), so sexual recombination was still expected to be rare. Additionally, from an analysis of laboratory crosses, it seems that only a small proportion of oospores is likely to germinate (6,18), so even if oospores are formed, the establishment of viable progeny in a field population may be rare.

Countering these factors, which are likely to limit the impact of sexual recombination in the population genetics of *P.*

infestans in the United States and Canada, is the very simple structure of most *P. infestans* populations in these countries. On potatoes, a single clonal lineage (US-8) dominates most populations (13). A few different clonal lineages have been found commonly on tomatoes, including US-6, US-7, US-11, and US-17 (7,9,13,14), but still most epidemic populations have been largely clonal and usually monomorphic. This very simple structure should enable easy detection of sexual progeny if they become established, and two epidemic populations resulting from sexual reproduction have been suggested: one for British Columbia and one for the Columbia Basin of Washington and Oregon (14,19). In the Columbia Basin, the putative sexual population was ephemeral, and now that location is nearly monomorphic for the US-8 clonal lineage (19).

One theory from evolutionary biology concerning the value of sexual reproduction applies particularly to the population structure of *P. infestans* in the United States and Canada. The "Red Queen" theory (25) suggests that in strongly clonal populations, sexual reproduction might rarely generate a new genotype (the "Red Queen") that is particularly fit and adapted to the current ecological conditions. This lineage could then dominate a population. It has been suggested, but not yet demonstrated, that certain lineages of *P. infestans* might have been generated by rare sexual recombination in the United States and Canada (13,14,19). Individuals from one of these populations (Columbia Basin of Washington and Oregon in 1993) have been stored and were available for additional study.

The objective of our investigation was to test the hypotheses that the population of *P. infestans* collected in the Columbia Basin in 1993 was generated by sexual recombination, and that one or more of the putative recombinants has been particularly dominant in certain agroecosystems. Our approaches were: (i) to add DNA fingerprinting alleles and mitochondrial haplotypes to the mating type and allozyme markers already reported for these isolates; (ii) to determine if the pattern of marker distribution was consistent with sexual

Corresponding author: W. E. Fry
E-mail: wef1@cornell.edu

Current address of P. D. Gavino: Boyce Thompson Institute for Plant Research, Ithaca, NY 14853.
Current address of R. W. Sandrock: Arcaris Inc., 615 Arapen Dr., Suite 300, Salt Lake City, UT 85108.
Current address of J. S. Miller: Department of Plant Pathology, University of Minnesota, St. Paul 55108-6030.
Current address of T. Yun Lee: Seoul National University, Suwon, Korea.

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recombinants; (iii) to compare the pattern of marker distribution in the field-collected isolates with the pattern in a set of progeny obtained from an in vitro mating between putative parents of the Columbia Basin isolates; and (iv) to compare the genotypes collected in the Columbia Basin with genotypes of isolates responsible for widespread epidemics in California in the spring and summer of 1998. Our aim was to determine if one of the suggested common clonal lineages might fit the criteria (rare fit genotype from sexual recombination that dominates a largely clonal population) for a "Red Queen."

MATERIALS AND METHODS

Characterization of isolates. Twenty-six isolates of *P. infestans* obtained from three adjacent counties in the Columbia Basin, and previously characterized (16,19) for mating type and genotype at the *glucose-6-phosphate isomerase* (*Gpi*) and *Peptidase* (*Pep*) loci were analyzed for additional markers. Bands at various nuclear DNA fingerprint loci were detected with probe RG57 using the method of Goodwin et al. (11). The mitochondrial DNA (mtDNA) haplotype was determined using the polymerase chain reaction-re-

striction fragment length polymorphism (PCR-RFLP) method described by Griffith and Shaw (15). Primer pairs 1, 2, and 4 designed by Griffith and Shaw (15) were used to amplify mtDNA regions by PCR. These primers are:

F1 - GCAATGGGTAAATCGGCTCAA;
R1 - AAACCATAAGGACCACACAT;
F2 - TTCCCTTTGTCTCTACCGAT;
R2 - GCTTATGCTTCAGTTGCTCAT;
F4 - TGGTCATCCAGAGGTTTATGTT;
R4 - CCGATACCGATACCAGCACAA.

Each PCR reaction (100 µl) consisted of 1× Thermo buffer (50 mM KCl, 10 mM Tris-HCl), 2.75 mM MgCl₂, 200 µM dNTPs, 0.325 µM each primer, 5 units of *Taq* DNA polymerase, and 100 ng of DNA. Amplification was conducted with one cycle of 94°C for 90 s followed by 40 cycles of 94°C for 40 s, 55°C for 60 s, and 72°C for 90 s (15). The PCR products were separated on 2% agarose gel and visualized with ethidium bromide stain following standard procedures (21). Products (P) were numbered according to the primer pairs used for amplification. Three products were digested with specific restriction enzymes. Products P1, P2, and P4 were digested with *Cfo*I, *Msp*I, and *Eco*RI, respectively. Haplotypes I-a, I-b, II-a, and II-b were identified by their restriction patterns as described by Griffith and Shaw (15) following the mtDNA nomenclature systems of Carter et al. (3). Some additional isolates stored in the *P. infestans* culture collection at Cornell were analyzed for reference using the techniques described above.

Analysis of progeny from a cross between US-6 and US-7. Because markers in the Columbia Basin isolates were all present in members of either the US-6 (A1) or US-7 (A2) clonal lineages, the pattern of nuclear and mitochondrial marker inheritance in progeny from a laboratory cross (no. 74 in the *P. infestans* culture collection at Cornell University) involving a strain of US-6 (US920159) and a strain of US-7 (US920219) was analyzed and compared with the genotypes of the Columbia Basin field isolates. Other characteristics of this cross had been reported previously (18). The segregation patterns for the two mating types (A1 and A2), bands at seven RG57 fingerprint loci, alleles at one allozyme locus (*Gpi*), and two mtDNA haplotypes (I-a and II-b) were recorded. However, because the GPI patterns resulting from genotypes 100/111 and 100/100/111 are usually very difficult to distinguish using cellulose acetate electrophoresis, all isolates that were heterozygous for GPI resulting from both the 100 and 111 alleles were recorded as 100/111.

Genetic characterization of *P. infestans* from California in 1998. Samples from a severe epidemic of late blight on tomatoes and potatoes in California in spring of 1998 were obtained and analyzed for genetic markers. Infected tomatoes or

potatoes were sent overnight to Cornell for analysis. The *Gpi* genotype was determined from all samples using the cellulose acetate method described by Goodwin et al. (12). As described above, there was no attempt to distinguish the 100/111 genotype from the 100/100/111 genotype. *P. infestans* was isolated into pure culture from most of the samples, and mating type, mitochondrial haplotype, and RG57 fingerprint were determined using techniques described above.

RESULTS

The 1993 isolates from the Columbia Basin contained individuals with diverse DNA fingerprints (Fig. 1) and two different mitochondrial haplotypes (I-a and II-b). The addition of these markers to the previously existing markers enabled the detection of 16 unique multilocus genotypes in this small population of 26 individuals (Table 1).

Five genotypes (1, 3, 4, 5, and 6) were found only in Morrow County, OR, and nine genotypes (7, 8, 9, 10, 11, 12, 13, 14, and 15) were found only in Umatilla County, OR (Table 1). One genotype (16) was detected in both Umatilla County and Walla Walla County, WA (Table 1).

Some genotypes collected in the Columbia Basin in 1993 had the same multilocus genotype as one of two previously described lineages. Genotype 1 (Table 1) had the same multilocus genotype as US-11 (Table 1, Fig. 1). Analysis of mtDNA from reference strains of the US-11 lineage revealed that this lineage has mtDNA haplotype II-b, the same as that of both the putative recombinant genotype 1 and the US-6 genotype (Tables 1 and 2). Genotype 10 had the same multilocus genotype as US-16, as described by Goodwin et al. (13).

There were several novel genotypes not previously recorded in the United States. These included genotypes 2, 3, 4, 5, 7, 8, and 9 (Table 1). Mitochondrial haplotype II-b had been detected previously, primarily in the US-6 clonal lineage (*unpublished results*), but it occurred in six genotypes in the Columbia Basin collection (1, 2, 3, 7, 8, and 9) (Table 1).

Pairs of polymorphic loci. Occurrence of recombination can sometimes be inferred if all possible recombinant genotypes occur for most pairs of polymorphic loci. Pairs of polymorphic nuclear loci (designated as present [1] or absent [0]) were identified in the RG57 fingerprint patterns of the putative recombinant genotypes. Despite the small sample size, all four possible genotypes (11, 10, 01, and 00) were detected when RG57 loci 5 and 6 are compared in the samples from Morrow County (Table 1). Similarly, all four possible genotypes occur for comparisons between loci 3 and 10, as well as between loci 7 and 10 (Table 1). In the samples from Umatilla County, all four possible

Fig. 1. Restriction fragment length polymorphism (RFLP) patterns obtained with probe RG57 via Southern analysis of isolates of *Phytophthora infestans* collected from the Columbia Basin of Washington and Oregon in 1993. Numbers at the tops of columns correspond to genotypes described in Table 1. (The US-8 isolate came from the culture collection at Cornell and was included for comparison purposes.) Numbers along the right-hand vertical axis are the RG57 band numbers.

Table 1. Recombinant genotypes of *Phytophthora infestans* obtained from the Columbia Basin of Washington and Oregon in 1993

nuDNA Genotype	Freq.	Location	Mating Type	<i>Gpi</i> Genotype ^b	mtDNA Haplotype	Nuclear (RG57) Fingerprint Loci ^c																								
						1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
1 (US-11)	2	Morrow	A1	100/111	II-b	1	0	1	0	1	1	1	0	0	1	0	0	1	1	0	1	0	1	0	1	0	0	1	1	
2	2	Morrow	A1	100/100	II-b	1	0	1	0	0	1	1	0	0	1	0	0	1	1	0	0	0	1	0	1	1	0	0	1	1
3	1	Morrow	A2	100/111	II-b	1	0	1	0	0	0	1	0	0	0	0	0	1	1	0	1	0	1	0	1	1	0	0	1	1
4	2	Morrow	A2	100/111	I-a	1	0	0	0	1	0	0	0	0	1	0	0	1	1	0	1	0	0	0	1	1	0	0	1	1
5	1	Morrow	A2	100/111	I-a	1	0	1	0	1	1	1	0	0	1	0	0	1	1	0	0	0	1	0	1	1	0	0	1	1
6	1	Morrow	A1	100/111	-	1	0	0	0	1	1	0	0	0	0	0	0	1	1	0	1	0	1	0	1	1	0	0	1	1
2	2	Umatilla	A1	100/100	II-b	1	0	1	0	0	1	1	0	0	1	0	0	1	1	0	0	0	1	0	1	1	0	0	1	1
7	1	Umatilla	A1	100/111	II-b	1	0	1	0	0	0	1	0	0	1	0	0	1	1	0	1	0	0	0	1	1	0	0	1	1
8	1	Umatilla	A1	100/111	II-b	1	0	1	0	0	0	1	0	0	1	0	0	1	1	0	0	0	1	0	1	1	0	0	1	1
9	1	Umatilla	A1	100/111	II-b	1	0	1	0	1	0	1	0	0	1	0	0	1	1	0	1	0	0	0	1	1	0	0	1	1
10 (US-16)	5	Umatilla	A1	100/111	I-a	1	0	0	0	1	1	0	0	0	1	0	0	1	1	0	1	0	1	0	1	1	0	0	1	1
11	1	Umatilla	A2	100/111	I-a	1	0	0	0	1	0	0	0	0	1	0	0	1	1	0	0	0	1	0	1	1	0	0	1	1
12	1	Umatilla	A1	100/111	I-a	1	0	0	0	1	0	0	0	0	1	0	0	1	1	0	1	0	1	0	1	1	0	0	1	1
13	1	Umatilla	A2	100/100	I-a	1	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	1	0	1	1	0	0	1	1
14	1	Umatilla	A1	100/111	-	1	0	1	0	1	0	1	0	0	1	0	0	1	1	0	1	0	1	0	1	1	0	0	1	1
15	1	Umatilla	A2	100/100	-	1	0	1	0	1	0	1	0	0	1	0	0	1	1	0	0	0	1	0	1	1	0	0	1	1
16	1	Umatilla	A1	100/111	I-a	1	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	1	0	1	1	0	0	1	1
16	1	Walla Walla	A1	100/111	I-a	1	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	1	0	1	1	0	0	1	1

^a Pairs of loci with four recombinant types in the samples from Morrow County, OR.^b *Glucose-6-phosphate isomerase* allozyme.^c Presence (1) or absence (0) of RG57 fingerprint bands 1-25.^d Pairs of loci with four recombinant types in the samples from Umatilla County, OR.**Table 2.** Analysis of a laboratory cross between US-6 and US-7 genotypes of *Phytophthora infestans*

Parental Isolates	Mating Type	<i>Gpi</i> Genotype ^b	mtDNA Haplotype	Nuclear (RG57) Fingerprint Loci ^c																								
				1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
US-6	A1	100/100	II-b	1	0	1	0	1	1	1	0	0	1	0	0	1	1	0	0	0	1	0	1	1	0	0	1	1
US-7	A2	100/111	I-a	1	0	0	0	1	0	0	0	0	0	0	0	1	1	0	1	0	1	0	1	1	0	0	1	1
Progeny																												
1	A1	100/111	II-b	1	0	1	0	0	1	1	0	0	0	0	0	1	1	0	0	0	1	0	1	1	0	0	1	1
2	A1	100/111	II-b	1	0	1	0	1	1	0	0	0	1	0	0	1	1	0	0	0	1	0	1	1	0	0	1	1
3	-	-	II-b	1	0	0	0	1	0	1	0	0	0	0	0	1	1	0	0	0	1	0	1	1	0	0	1	1
4	A2	100/100	II-b	1	0	1	0	0	0	1	0	0	1	0	0	1	1	0	1	0	0	0	1	1	0	0	1	1
5	-	100/100	II-b	1	0	0	0	1	1	0	0	0	1	0	0	1	1	0	1	0	1	0	1	1	0	0	1	1
6	-	100/111	II-b	1	0	0	0	1	0	0	0	0	1	0	0	1	1	0	0	0	1	0	1	1	0	0	1	1
7	A1	100/111	II-b	1	0	1	0	1	0	1	0	0	0	0	0	1	1	0	0	0	1	0	1	1	0	0	1	1
8	A1	100/111	II-b	1	0	1	0	1	1	1	0	0	1	0	0	1	1	0	0	0	1	0	1	1	0	0	1	1
9	A1	100/111	II-b	1	0	0	0	1	0	0	0	0	1	0	0	1	1	0	1	0	1	0	1	1	0	0	1	1
10	A1	100/111	I-a	1	0	1	0	0	1	0	0	0	0	0	0	1	1	0	0	0	1	0	1	1	0	0	1	1
11	A1	100/111	I-a	1	0	1	0	1	1	1	0	0	1	0	0	1	1	0	0	0	1	0	1	1	0	0	1	1
12	A2	100/100	I-a	1	0	1	0	0	1	1	0	0	0	0	0	1	1	0	1	0	0	0	1	1	0	0	1	1
13	A2	100/100	I-a	1	0	0	0	0	0	1	0	0	1	0	0	1	1	0	1	0	0	0	1	1	0	0	1	1

^a Pairs of loci with four recombinant types similar to the 1993 samples from Morrow County, OR.^b *Glucose-6-phosphate isomerase* allozyme.^c Presence (1) or absence (0) of RG57 fingerprint bands 1-25.^d Pairs of loci with four recombinant types similar to the 1993 samples from Umatilla County, OR.

genotypes occur for loci 3 and 5 and loci 7 and 16 (Table 1).

Similarities among recombinant genotypes from an in vitro laboratory cross and isolates from the field. The segregation pattern of nuclear and mitochondrial markers in the field isolates was similar to that observed in the progeny ($n = 13$) from a cross between US-6 and US-7 (Table 2). Only *Gpi* alleles 100 and 111 occurred in both the field isolates and laboratory progeny. The four recombinant genotypes (11, 10, 01, and 00) for RG57 loci 3 and 5, as well as for loci 7 and 16, were observed in both the laboratory progeny and the field isolates from Umatilla (Tables 1 and 2). Additionally, the four recombinant genotypes for loci 5 and 6, for loci 3 and 10, and for loci 7 and 10 were observed in the laboratory progeny and in the field isolates from Morrow (Tables 1 and 2). Sexual recombination distributed both mtDNA haplotypes to both A1 and A2 progeny in the laboratory cross (Table 2); and likewise in the field isolates, both A1 and A2 isolates had either mtDNA haplotype (Table 1).

Late blight epidemic in California 1998. Late blight on tomatoes and potatoes was severe in the spring of 1998 in California. Samples ($n = 47$) from 24 counties (Fig. 2) were received and analyzed for *Gpi* genotype directly from tissue. Of these, all 40 samples from tomatoes had the 100/111 *Gpi* genotype that is characteristic of the US-11 lineage (making no attempt to distinguish the 100/111 genotype from the 100/100/111 genotype). From potatoes, six samples also had the *Gpi* genotype 100/111 characteristic of the US-

11 lineage, and one had the 100/111/122 *Gpi* genotype characteristic of the US-8 lineage. Pure cultures of 44 of the 47 samples were obtained and analyzed for RG57 fingerprint, mating type, and mtDNA haplotype. All 43 isolates with the 100/111 *Gpi* genotype had the RG57 fingerprint typical of the US-11 lineage, were A1 mating type with mt haplotype II-b, and therefore belonged to the US-11 lineage. The isolate with the 100/111/122 *Gpi* genotype had the RG57 fingerprint typical of the US-8 lineage, was A2 mating type with mitochondrial haplotype I-a, and therefore belonged to the US-8 lineage.

DISCUSSION

The pattern of polymorphisms in nuclear markers, mating type, and mtDNA haplotypes in the isolates of *P. infestans* collected in the Columbia Basin in 1993 provided strong genetic evidence that these were progeny of a sexual recombination event. Several criteria for sexual reproduction were satisfied. First, isolates of both mating types occurred in the same general region—a situation that has been rare in the United States and Canada during the 1990s (7,13). Second, the genotypic diversity in this population was much greater than that seen prior to and following the epidemic in the Columbia Basin in 1993 (19) and greater than has been the case for most other collections of *P. infestans* in the United States and Canada. After 1994, the population of *P. infestans* in the Columbia Basin was dominated by the US-8 clonal lineage (19). Third, this population contained individuals with two different mtDNA haplotypes: haplotype I-a, characteristic of recently introduced strains from Mexico, and haplotype II-b, which previously had been detected only in the US-6 clonal lineage (8). The mitochondrion is uniparentally inherited in *Phytophthora* (24), so some progeny would be expected to have mtDNA from one parent, and other progeny would have the mtDNA from the other parent. If the parental strains were US-6 and US-7, the two mitochondrial haplotypes would be II-b (US-6) and I-a (US-7). The US-6 clonal lineage was common in the Pacific Northwest prior to 1993. And fourth, the pattern of polymorphisms at many paired loci had all possible allelic combinations. This pattern has been used previously to infer sexual recombination in fungal populations such as those of *Coccidioides immitis*, *Armillaria gallica*, and *Sclerotinia sclerotiorum* (1,2,22).

Additionally, there were remarkable similarities between the field population isolates and the progeny of a cross between the putative parents of the field population. We hypothesize that the parents for the field population were US-6 (A1) and US-7 (A2). The “private” alleles (those confined to a particular lineage) (RG57 band 6 and the mtDNA haplotype II-b) in US-6 were present in the field population. Private

alleles specific to other clonal lineages, such as RG57 bands 9 and 23 (in US-8 and US-1), as well as *Gpi* alleles 86 (US-1) and 122 (US-8), were not found among the field isolates (Table 1). *Gpi* alleles 100 and 111, present in US-6 and US-7, were the only ones in the field isolates. The mtDNA haplotypes II-b (US-6) and I-a (US-7) were inherited in the lab progeny and occurred in novel genotypes in the same manner as in field recombinants (Tables 1 and 2). There were striking similarities when the pairs of polymorphic loci were compared. For example, the four recombinant genotypes (11, 10, 01, and 00) were present in pairing loci 3 and 10 and loci 7 and 16 in the lab progeny as well as in the field recombinants (Tables 1 and 2). The US-6 specific alleles at RG57 band 6 occurred in the field progeny in the same combinations as they did in the laboratory progeny (Tables 1 and 2).

The actual location and date of the field sexual recombination event cannot be determined from the data available. It is possible that oospores were formed in the Columbia Basin, but it is also possible that they were formed elsewhere and the progeny were introduced to the Columbia Basin. The introduction could have been as oospores or as mycelium in infected plants or in infected seed tubers. However, we hypothesize that the coherence of the cohort in 1993 and its subsequent dissolution suggest that the production and germination of oospores occurred shortly before the 1993 isolates were collected. Despite this, we expect that selection had already operated on this population prior to collection so that the field collection would not necessarily have all possible representatives of recombination.

It is improbable that either mutation or diverse migrations caused the high degree of genotypic diversity in the 1993 population from the Columbia Basin. Although there can be rare mutations in fingerprint alleles within a clonal lineage, the allozyme alleles, mating type, and mtDNA have been generally consistent over time (10). It is unlikely that multiple mutations occurred spontaneously in such a small sample of isolates. Migration of this diverse a population has not been observed elsewhere in the United States or Canada. While migrations are well documented in the United States and Canada, typically they have involved movement of single clonal lineages from known sources (7). Most of the diverse isolates have not been detected elsewhere, and those that have been were detected subsequent to 1993. It also appears unlikely that migration of this cohort from northwestern Mexico (the probable source of US-6 and US-7) is the origin of the population. The cohort is associated with potatoes, and potatoes are not imported from Mexico to the United States. Populations of *P. infestans* from northwestern Mexico have been highly

Fig. 2. Locations (by county in California) in which the US-11 lineage (gray areas) and the US-8 lineage (black areas) of *Phytophthora infestans* were found in 1998. Only one isolate of the US-8 lineage was detected, and the checkerboard pattern indicates that both US-11 and US-8 were detected in one county.

clonal with very few lineages detected (*unpublished results*), and no evidence of sexual reproduction has been detected there. The rapid disappearance of the diversity in *P. infestans* in the Columbia Basin after 1993 is consistent with the hypothesis that the germination of oospores occurred shortly before the isolates were collected, and that the cohort remained at least partially intact during 1993, but not subsequently.

Thus, the results of our analyses are consistent with the hypothesis that the US-11 lineage originated as an especially fit sexual recombinant in the United States. The first occurrence of this lineage was in a collection of diverse individuals collected in the Columbia Basin in 1993, which together had the characteristics of a sexual progeny. Subsequently, this lineage has been dominant in western Washington, where it is pathogenic on both potatoes and tomatoes (5); however, in contrast to the US-8 clonal lineage, US-11 has been particularly troublesome on tomatoes as well as on potatoes (5; *unpublished results*). The fitness of the US-11 clonal lineage is certainly high for certain agroecosystems, particularly those with tomatoes. In contrast to the other genotypes detected in the 1993 Columbia Basin epidemic, the US-11 lineage has been common in the Pacific Northwest since 1994 (5,13), occurred in New York State on tomatoes in 1998 (*unpublished results*), and caused severe epidemics on greenhouse and field-grown tomatoes in California in the spring of 1998 (this report). Thus, we conclude that this lineage fits the criteria describing a "Red Queen"—an individual resulting from sexual reproduction that can dominate a population of an asexually reproducing organism. As such, it demonstrates that one of the fears for the occurrence of sexual reproduction of *P. infestans* in the United States (generation of aggressive lineages) has been realized.

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