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THE BIOLOGY OF *PHYTOPHTHORA INFESTANS* AT ITS CENTER OF ORIGIN*

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■ **Abstract** The central highlands of Mexico are considered to be a center of genetic diversity for both the potato late blight pathogen and for tuber-bearing *Solanum* spp. Recent work conducted in Mexico and South America sheds new light on the biology and evolution of *Phytophthora infestans* and other related *Phytophthora* pathogens. It now appears that Mexican *Solanum* species, which coevolved with *P. infestans* and were previously known for providing a source of R-genes, also provide a source of quantitative, rate-reducing resistance that is highly effective, stable, and durable. It is now apparent that Mexico is the center of origin not only of the potato late blight pathogen *P. infestans*, but also of several related *Phytophthora* species including *P. mirabilis*, *P. ipomoeae*, and possibly *P. phaseoli.* We close with the hypothesis that these *Phytophthora* species evolved sympatrically from one ancestral host through adaptive radiation onto their respective four host families.

INTRODUCTION

Potato late blight continues to be one of the most important crop diseases of all time. Best known for its role in causing the Irish potato famine in the 1840s, it is still responsible for significant losses and increases production costs through the need for recurrent fungicide usage, annual reductions in marketable yields, and postharvest losses. Potato late blight is caused by the oomycete plant pathogen *Phytophthora infestans* (Mont.) de Bary. The central highlands of Mexico are considered to be a center of genetic diversity for both the potato late blight pathogen (21, 26, 36, 40) and for germplasm of tuber-bearing *Solanum* spp. (46, 48, 79–81). R-genes for resistance to potato late blight were first discovered in two endemic *Solanum* species, namely *S. demissum* and *S. stoloniferum* (56, 60, 61). The presence of

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R-genes is the result of coevolution between *P. infestans* and native *Solanum* spp. (82). As the discovery of R-gene diversity in native *Solanum* spp. and genotypic diversity in the *P. infestans* population coincided, the hypothesis was advanced that Mexico might be the center of origin of *P. infestans* (27). Recent work conducted in Mexico and South America sheds new light on the biology and evolution of *P. infestans* and related, endemic sister species. In this review we focus on the natural history, ecology, host resistance as well as evolution of *P. infestans* and closely related *Phytophthora* species in central Mexico. We end by advancing the hypothesis that a specific group of Mexican *Phytophthora* species, to date including *P. mirabilis*, *P. ipomoeae*, *P. phaseoli*, and *P. infestans*, share one common ancestor and are the result of evolution through sympatric speciation.

NATURAL HISTORY AND EPIDEMIOLOGY

Foliar Epidemics

Epidemic development of potato late blight critically depends on the local climate. Our current understanding of the epidemiology of potato late blight is strongly biased by studies conducted in regions with temperate climates. Areas of the highland tropics, including the central highlands of Mexico, have a very different climate. Most potato late blight research conducted in Mexico took place in the Toluca valley because the Mexican national potato program is located there. This valley offers a typical tropical highland climate given the elevation (>2600 m above sea level), latitude (19°N), and longitude (99°E). In contrast to a typical temperate climate, Toluca summers are characterized by almost constant cool temperatures and almost daily precipitation (41, 42). Typically, between 800 to 900 mm of rainfall are recorded yearly, most of which occurs during July to September, and daily mean temperatures remain between 5° to 10°C with daily maxima around 20° to 25°C, providing cool night and day temperatures (41, 42). The number of hours with relative humidity above 90%, a surrogate measure for hours of leaf wetness, generally ranges between 12 to 16 h on 75 to 90% of days. Given the daily precipitation and cool temperatures, this climate is favorable to late blight development on almost every day of the growing season.

Late blight epidemics on commercial potatoes in the Toluca valley are driven by the onset of the rainy season. Potatoes are usually planted in early to mid June, just 2 to 4 weeks before the daily rains begin. Once the rainy season starts, epidemics are initiated on emerging plants, and disease on a susceptible cultivar such as Alpha progresses steadily, typically resulting in a logistic disease progress curve (41, 42, 66). In contrast, epidemics on native *Solanum* species follow a different dynamic.

Epidemics on wild *Solanum* spp. rarely occur before the end of August or beginning of September (40). As discussed below, several factors might contribute to this observation including the small size and patchy distribution of *Solanum* populations as well as the R-gene structure and distribution. Rivera-Peña (66) describes development of epidemics on *S. demisssum* and *S. verrucosum* as early as late June to early July, generally 3 weeks after symptoms are observed on

cultivated potato in the vicinity. Thus, epidemics on native *Solanum* spp. might well derive initial inoculum from nearby epidemics on cultivated potato.

Forecasting systems for control of potato late blight were developed for the temperate climates of Europe and the United States, and it is not clear how portable they are to the highland tropics. While evaluating several forecasting systems (6, 10, 74) for management of fungicides to control late blight under Toluca valley conditions, we noticed that initial spray advisories usually occurred 8 to 15 days too late (42) and that precipitation was the main environmental variable responsible for making spray advisories (41). A series of simulations based on historical weather data showed that the assumptions for low-temperature thresholds in these models were not valid in Toluca. Whereas the forecasting algorithms developed for temperate climates assume no pathogen development at temperatures below 7°C (50), 8°C (16), or 10°C (6, 10, 25, 74), it is clear that *P. infestans* develops at these temperatures (4, 41, 42). Such low temperatures are regularly achieved; for example, 58% of days had hourly temperatures $\leq$10°C and 10% of days had hourly temperatures $\leq$7.2°C in 1998. The temperature response of *P. infestans*, as implemented in commonly used disease forecasting systems, thus needed to be reassessed for the Toluca valley. This work demonstrated that a predictive system developed for temperate climates can be portable to a tropical highland climate based on just a few minor modifications (41).

Tuber Blight

Tuber blight is a critical stage in the late blight disease cycle, resulting in postharvest yield loss and serving as a source of inoculum. Tuber blight is common in the Toluca valley and occurs when severe late blight epidemics coincide with heavy rainfall and waterlogging. Lapwood (52) first reported on the incidence of tuber blight in fungicide-protected crops in the Toluca valley and observed 1 to 13% blighted tubers in cultivars Majestic and Elenita. Fernández-Pavía (19) reported 4% blighted tubers in cv. Alpha grown at Calimaya, Mexico. At an experimental field in Metepec, Mexico tuber blight incidence in 1999 ranged from 0 to 15%, confirming previous observations (N.J. Grünwald & W.G. Flier, unpublished data). Not much is known about the extent to which *P. infestans* survives the crop-free period in terms of hibernation in seed or volunteer tubers. From our experience, it seems unlikely that *P. infestans* is able to survive in seed tubers, given current seed-storage conditions. Most storage facilities use ambient temperatures to store tubers, and blighted tubers generally rot completely during storage. Thus, tubers going to the field in the next growing season are usually free of late blight. Infected tubers and stolons do not appear to play a role in the life cycle of *P. infestans* on wild solanaceous hosts in the Toluca valley as no blighted stolons or tubers were detected in our own observations and those of Lapwood (52) and Rivera-Peña (65).

Fungicide Resistance

Potato production in Mexico relies heavily on fungicides given the annual severe late blight pressure (41, 42). Mancozeb is the most commonly used fungicide.

However, metalaxyl has been used in the past and continues to be used sporadically. There are two interesting observations regarding metalaxyl resistance in the Mexican population. First, there exists a baseline level of resistance even when the pathogen population has not been exposed to metalaxyl; second, once exposed, the population undergoes selection, but also fairly rapidly reverts to pre-exposure threshold levels. Resistance to metalaxyl evolved rapidly in the Mexican population of *P. infestans* after introduction of metalaxyl (55) but then reverted to resistance levels found previous to the introduction (40). For example, metalaxyl resistance was much less frequent in a 1997–1998 than in a 1988–1989 collection (reported in 55). The proportion of isolates that grew more than 40% of the control on 5 and 100 μg ml^{-1} metalaxyl-amended medium was much lower for isolates collected in 1997–1998 (13%) than for isolates collected in 1988–1989 (60%). By 1997–1998, the frequency distribution is again similar to frequencies of metalaxyl resistance observed in central Mexico in the early 1980s before metalaxyl use (55).

We also evaluated whether selection for resistance to metalaxyl and cymoxanil could evolve under experimental conditions within a single field season. We contrasted populations before and after fungicide exposure following seven fungicide applications during the field season in 2000. Significance of shifts in sensitivity profiles to each of the fungicides was determined using Fisher's exact test ($n = 50$ isolates). The frequency distributions for metalaxyl and cymoxanil resistance significantly ($P < 0.0011$ and 0.0001, respectively) shifted to the right as reflected by the median for each population (Figure 1), indicating directional selection toward resistance. However, selection toward resistance combined with a significant reduction in genetic diversity ($P < 0.01$) based on multilocus genotypes (mating type, *Pep*, and *Gpi*) using Shannon-Wiener's diversity index of the population of *P. infestans* after exposure ($H' = 1.8$) relative to the unexposed population ($H' = 2.6$) was observed only for metalaxyl. It thus appears that at least for the case of metalaxyl, exposure to multiple applications of metalaxyl resulted in purifying selection and a concomitant reduction in genotypic diversity.

Oospores

Oospores are the sexual reproductive spores formed by *P. infestans.* In the Toluca valley, oospores are ubiquitous and are formed in all tissues examined to date. Oospore formation has been detected in potato leaflets of commercially grown field crops (30, 75), in infected leaflets of the native species *S. demissum* (20), and in potato tubers (19). The densities of oospores produced range from a few to over 5000 per cm^2 for infected potato tubers and leaflets of *S. demissum*, respectively. The distribution of oospores in infected leaflets appears to be confined to one or a few clusters per leaflet (20).

Many factors affect oospore formation. The ability of compatible isolates to form oospores in both artificial media (2, 20, 28, 30, 49, 72, 73, 75, 77, 78) and host tissues (20, 57) seems to vary among combinations of parental strains. There also is a range of preference to serve as the male or female parent depending on the

parental isolates (28, 49). Formation of oospores may also be influenced by host resistance. Under field conditions in central Mexico, it appears that the greatest numbers of oospores are produced in potato cultivars with intermediate levels of late blight resistance (17; W.G. Flier, unpublished data), although other modulating factors may be involved (45, 87).

Oospores are thought to have two main functions in the life cycle of *P. infestans*: First, they provide a means of survival and thus could serve as primary inoculum for epidemic development; second, they provide a means of sexual recombination (discussed further in the section on population biology). Lapwood (52) suggested that oospores were the most plausible source of primary inoculum in the Toluca valley. Primary infections appeared either as stem lesions that extended only a few centimeters below the soil surface or as multiple lesions on lower leaves. These lesions were randomly distributed in a field and were first observed after heavy rains. No other potential sources of initial inoculum such as infected seed, cull piles, or nearby infected wild *Solanum* species were observed (52). These early observations accurately describe the current situation. During a three-year survey (1997–1999) in the Toluca valley and the slopes of the volcano Nevado de Toluca, we found the same type of stem and foliar lesions (20). Experimental work demonstrated that soil infested with oospores resulted in a significantly higher number of primary stem lesions compared with noninfested soil (18). This work also confirmed that oospores of *P. infestans* can survive winter fallow and subsequently infect field crops under natural conditions (18, 19).

Oospores of *P. infestans* seem very well adapted to the local conditions. They are produced in large numbers in all tissues of infected potato crops and wild solanaceous hosts and are eventually incorporated into the soil with the crop debris. In the Toluca valley, winters are marked by a cool and dry climate favorable to the survival of dormant oospores. Presumably, oospores incorporated into soil are not subject to microbial degradation and premature germination during the winter while soils remain dry. A subsequent potato crop planted at the end of the dry season coincides with germination of oospores once soils become moist (3, 15, 87). It appears that the life cycle of both host and pathogen are synchronized to the local climatic conditions.

INDIGENOUS *SOLANUM* SPECIES

Central Mexico is considered to be a secondary center of diversity for the genus *Solanum* (46, 48). Several tuber-bearing *Solanum* species are endemic to the Toluca valley: *S. demissum* Lindt., *S. verrucosum* Schlechtd., *S. iopetalum* (Bitt.) Hawkes, *S. brachycarpum* Correll, *S.* × *edinense* Berth., and *S. stoloniferum* Schlechtd. et Bché. (64, 68). Rivera Peña (68), surveying an area of approximately 15,000 ha, estimated that *S. demissum* was most frequent (69%), followed by *S. verrucosum* (11%) and the other five species. From previous studies and our own observations (Table 1), it is clear that all of these native species can be infected by *P. infestans*

TABLE 1 Final disease severity of different *Solanum* accessions and nightshade species in experimental plots planted in Toluca, Mexico

Accession	Species	Origin	Source of data	Final disease severity (%)	Isolates obtained
CGN-18,162	*Solanum acaule*	South America	Grünwald & Flier, unpublished data	95	Yes
CGN-20,675	*Solanum acaule*	South America	Grünwald & Flier, unpublished data	100	Yes
CGN-17,845	*Solanum acaule*	South America	Grünwald & Flier, unpublished data	40	Yes
CGN-18,344	*Solanum andreanum*	South America	Grünwald & Flier, unpublished data	8	Yes
CGN-18,311	*Solanum bulbocastanum*	Central America	Grünwald & Flier, unpublished data	1	Yes
CGN-17,688	*Solanum bulbocastanum*	Central America	Grünwald & Flier, unpublished data	8	No
—	*Solanum bulbocastanum*	Central America	(53)	12–15	No
93,046	*Solanum caripense*	South America	Grünwald & Flier, unpublished data	25	Yes

—	*Solanum demissum*	Central America	(53)	7–34	No
—	*Solanum iopetalum*	Central America	(53)	0–8	No
CGN-18,303	*Solanum phureja*	South America	Grünwald & Flier, unpublished data	100	Yes
CGN-18,340	*Solanum phureja*	South America	Grünwald & Flier, unpublished data	100	Yes
CGN-18,281	*Solanum phureja*	South America	Grünwald & Flier, unpublished data	90	Yes
CGN-17,670	*Solanum phureja*	South America	Grünwald & Flier, unpublished data	40	Yes
CGN-18,315	*Solanum phureja*	South America	Grünwald & Flier, unpublished data	40	Yes
CGN-19,135	*Lycopersicum esculentum* var. Bonny Best	—	Grünwald & Flier, unpublished data	78	Yes
—	*Nicotiana glauca*	—	Grünwald, unpublished data	0	No
—	*Nicotiana benthamiana*	—	Grünwald, unpublished data	0	No

(53, 65). Approximately 10% of these native plants became infected in a given year (65). Many of these *Solanum* spp. occur in small populations in a range from fewer than a dozen individuals up to a few hundred plants. This patchiness and spatial isolation from potato-growing areas allows them to avoid infection by *P. infestans.* Patches can be assumed to consist of predominantly one or a few host clones harboring limited combinations of R-genes, since all plants of native *Solanum* spp. uprooted by us or in a previous study (66) were found to originate from tubers. One exception is the hybrid *S.* × *edinense* that is predominantly associated with low-input potato fields where growers keep seed tubers for the next potato crop.

All tuber-bearing *Solanum* spp. of South or Central American origin are susceptible to *P. infestans* to some degree. When grown in experimental plots, disease incidence is 100% and disease severity can range anywhere from 1 to 100% depending on the species and R-gene makeup of the individual genotype (Table 1) (53). This may be a result of the fact that levels of rate-reducing resistance and composition of R-genes vary among specific genotypes within a *Solanum* spp. and among *Solanum* spp. (9, 53, 54, 67). Epidemics on wild *Solanum* species under controlled experimental conditions progress in the same fashion as those on cultivated potato once initiated.

CAN HOST RESISTANCE BE STABLE AND DURABLE?

The search for host resistance genes that provide immunity against potato late blight has centered on Mexico for some time. It was here that the first 11 R-genes for resistance to late blight were discovered in two native species, namely *S. demissum* and *S. stoloniferum* (56, 60, 61). It soon became clear that gene-for-gene resistance was not the solution to management of potato late blight as R-gene resistance was easily overcome. Breeders in Mexico thus concentrated on developing cultivars with rate-reducing resistance (59, 83, 88). One result of these interests was a series of breeding lines and clones developed by the Rockefeller Foundation and the Mexican national potato breeding program that relied on the introduction of field resistance from native *Solanum* species. This research program has produced several cultivars with remarkably high levels of field resistance (23, 24, 39, 41, 42). Cultivars such as Sangema (also known as Rosita) and Norteña show very high levels of field resistance, resulting in less than 25% or 8% foliar disease severity, respectively, without the use of a fungicide under Toluca valley conditions (41, 42). In a recent study, 12 of these Mexican cultivars were evaluated for durability of resistance to late blight based on experimental data recorded between 1960 and 1999 (39). At least two of these cultivars (Sangema and Tollocan) were grown on at least 5% of the potato acreage and over long periods of time without an apparent decay in field resistance, indicating that this field resistance is durable. Pedigrees of these 12 cultivars indicate that this field resistance was introgressed from *S. demissum* and possibly from local varieties such as 'Amarilla de Puebla' and 'Leona'. Thus, it appears that potatoes that show stable and durable resistance under tropical highland conditions are available (39).

A novel R-gene has recently been identified from *Solanum bulbocastanum*, another *Solanum* spp. native to Mexico (47, 89). The R-gene from *S. bulbocastanum* may be of a more general nature than R-gene resistance derived from *S. demissum*, as sporulation on *S. bulbocastanum* under Toluca valley conditions is limited to small, often necrotic lesions that sporulate at low frequency (47; N.J. Grünwald, unpublished data). Two allelic versions, RB and *Rpi-blb1*, of the R-gene have been mapped and cloned (58, 76, 89) and have provided renewed hope that monogenic resistance might be useful in managing potato late blight. Whether these novel R-genes will provide stable and durable resistance to late blight in a *S. tuberosum* background remains to be seen, given our previous experience with monogenic resistance to late blight. Certainly, the RB gene looks promising under Toluca valley conditions when exposed to a genetically diverse pathogen population.

PHYTOPHTHORA POPULATION BIOLOGY

Genotypic Variation and Marker Systems in *P. infestans*

As discussed above, oospores are formed ubiquitously and are expected to result in higher levels of genotypic variation in local populations of *P. infestans*. It appears that, unlike other populations of *P. infestans*, most isolates from central Mexico are diploid, with the exception of a few aneuploid strains. In an early study, Sansome (69) reported that Mexican isolates had a chromosome number approximately half that of isolates from North Wales. This was later confirmed by nuclear DNA content studies by Tooley & Therrien (86) and Gu et al. (43) using Feulgen and DAPI staining techniques, respectively.

A range of genotypic and phenotypic marker systems have been used to study diversity in populations of *P. infestans* from Mexico. The first studies relied on determination of virulence phenotype, mating type, and allozyme genotype. The population of *P. infestans* in central Mexico differs from other populations by the frequencies of specific virulence factors. More complex races, including isolates containing all of the specific virulence factors detectable (race 1.2.3.4.5.6.7.8.9.10.11), were found in isolates sampled from wild *Solanum* species and experimental potato fields (64). In most studies, mating-type ratios followed a 1:1 ratio and allozyme genotypes were in Hardy Weinberg equilibrium (36, 40), as expected for randomly mating populations. The moderately repetitive RFLP fingerprinting probe RG57 (33) allowed for the resolution of up to 27 distinct genetic loci, with every isolate obtained from Toluca having a unique banding pattern (36). More recently, amplified fragment length polymorphism (AFLP) was added to the repertoire of marker systems (21, 40). AFLP fingerprinting of 170 isolates collected in 1997 yielded 158 distinct loci of which 135 were polymorphic (21). High levels of genetic variation for a range of marker systems in *P. infestans* are clearly in evidence, whether isolates are derived from single lesions in a plot, a field, or the whole valley of Toluca (21, 33, 37, 40, 84, 85).

Population Differentiation in *P. infestans*

There have been recent efforts to describe the population structure of *P. infestans* within the Toluca valley. Based on our knowledge of the natural history of the valley, it was apparent that this population could potentially be differentiated by up to three habitats based on host-plant and potato production systems (40). In the valley, intensive potato production with high inputs of pesticides and fertilizers is the norm. Low-input potato production is found on the foothills of the volcano Nevado de Toluca where potatoes are grown for subsistence. A third habitat for *P. infestans* is provided by several of the native *Solanum* species (68). No clear spatio-temporal discontinuity is present between cultivated potatoes in agroecosystems and wild *Solanum* hosts in natural ecosystems in the Toluca valley. The growing season for both cultivated and wild hosts is restricted to the summer season. Two endemic *Solanum* spp., *S. stoloniferum* and the hybrid species *S.* × *edinense*, occur in potato fields and other disturbed areas such as roadsides. At higher elevations in less disturbed ecosystems, wild *Solanum* species are found in forests dominated by *Abies* spp. and in extensively grazed grasslands.

Based on this knowledge of *P. infestans*, we tested the hypothesis that its populations in the Toluca valley are differentiated by the three habitats. All genetic marker systems, including allozyme, RFLP, and AFLP data, revealed significant differentiation by habitat (21, 40). The population structure seems to be fairly stable over time as it remained similarly differentiated between two large population samples obtained in 1988/89 and 1997/98 (40). Allozyme data indicated that heterozygosity and genotypic diversity in populations of *P. infestans* declined from commercial potato fields to wild *Solanum* spp. (40).

The picture was further refined in a follow-up study where AFLP data revealed an increase in genotypic diversity in the wild *Solanum* habitat (21). Subpopulations of *P. infestans* found in this habitat were among the most variable populations found in the valley. AFLP analysis revealed the presence of a large number of private alleles and highest heterozygosity in the native *Solanum* spp. subpopulation. On average, migration was less than 1 migrant per generation between populations of *P. infestans* from potatoes and of *S. demissum*, whereas no restrictions in gene flow were measured between populations of *P. infestans* from high- and low-input potato production systems. Thus, the conclusions drawn from these two studies differed slightly in interpretation of the direction of gene flow: Where the allozyme markers indicated a flow from high-input potatoes via low-input potatoes to native *Solanum* habitats (40), the opposite was the case when interpreting AFLP data (21).

The interpretations in the first study critically depended on the patterns observed for the selectable marker metalaxyl resistance. Metalaxyl-resistant strains were found on commercial potato crops and native *Solanum* species in similar frequencies, suggesting that strains migrate freely between potato crops and native *Solanum* species (40, 55). At the time, we assumed that any resistance to metalaxyl was the result of selection; as discussed above, we now believe that there exists a

baseline frequency of resistance as observed before the introduction of metalaxyl (55).

The reinterpretation of population structure based on metalaxyl resistance is also supported by observations on oospore formation. Differences in oospore production were observed between in vitro crosses of strains of *P. infestans* collected from potato and *S. demissum*. Isolates originating from the native host *S. demissum* produced significantly more oospores in crosses with strains collected from the same host species compared with crosses with isolates collected from cultivated potatoes (20).

The population structure of *P. infestans* in the Toluca valley is structured by several forces and has the appearance of a metapopulation structure on the native *Solanum* host species. This metapopulation provides a habitat for *P. infestans* consisting of small, random R-gene-driven islands that only phenotypes with compatible virulence genes can colonize. Furthermore, the patchiness of the native host population of *Solanum* reduces the effective population size of *P. infestans* in that habitat, thus resulting in genetic drift. At the same time, all three habitats are connected by gene flow, and the importance of individual forces remains to be established.

Genotypic Diversity in *Phytophthora* Species Related to *P. infestans*

As outlined under speciation below, *P. infestans* has four close relatives coexisting in central Mexico. Two obvious questions emerging from the genotypic diversity work on *P. infestans* were whether the same markers show polymorphism in these relatives, namely *P. phaseoli*, *P. mirabilis*, and *P. ipomoeae*, and whether the populations are equally diverse. In a moderate size collection of isolates ($n = 58$) of *P. mirabilis* sampled in Toluca and neighboring valleys, we detected no polymorphism at the *Pep* locus (fixation of the 96/96 genotype), 12 *Gpi* genotypes (including alleles 83, 90, 100, 108, and 111), 7 RFLP genotypes ($n = 37$), and a total of 23 multilocus genotypes ($n = 37$) based on mating type and *Gpi* (N.J. Grünwald, unpublished data). Similarly, a population ($n = 14$) of *P. ipomoeae* was polymorphic for both the *Pep* (78/78, 78/96, 96/96) and *Gpi* (96/108, 108/108) loci, and we obtained 4 multilocus genotypes based on these two markers, whereas only one RFLP genotype was detected (22; N.J. Grünwald & W.G. Flier, unpublished data). Goodwin had previously established that the RG-57 RFLP probe is both evolutionarily conserved and highly polymorphic among close relatives of *P. infestans* including *P. mirabilis*, *P. colocasiae*, and *P. phaseoli* (33). AFLP fingerprinting revealed limited genetic variation in isolates of *P. ipomoeae*. Seven AFLP genotypes were found in a sample of 10 isolates (W.G. Flier, unpublished data). Thus, the molecular markers chosen for *P. infestans* based on their polymorphism are also polymorphic for *P. mirabilis* and *P. ipomoeae*, although less so. This is to be expected as the markers used for *P. infestans* were selected to be the most polymorphic for that organism, but not for the other two *Phytophthora* species.

mtDNA Haplotype Diversity in *P. infestans* and Relatives

Currently, four mitochondrial haplotypes are described for *P. infestans* designated as Ia, Ib, IIa, and IIb (13, 38, 63). Isolates of the US-1 genotype show the Ib mtDNA haplotype (13, 38). The Ia mtDNA haplotype was the predominant haplotype found in the Toluca valley, although the IIa and IIb haplotypes were also observed in Mexico (31, 32). Because the Ib haplotype of the ancestral US-1 strain was not observed in Mexico, some studies hypothesized that the center of origin of *P. infestans* might be found in South America (62, 63). Recently, S.P. Fernández-Pavía and W.G. Flier (unpublished data) discovered the Ib haplotype in two Mexican isolates collected in 2003 in central Mexico. This discovery of the Ib haplotype in Mexico provides renewed evidence that the centers of diversity and origin of *P. infestans* coincide and are found in the central highlands of Mexico.

All three *P. infestans* relatives have one or more species-specific mtDNA haplotype(s) that are based on RFLPs (Figure 2). Although four haplotypes have been reported for *P. infestans*, only one mtDNA haplotype has been reported for *P. mirabilis* and *P. ipomoeae*, respectively (22).

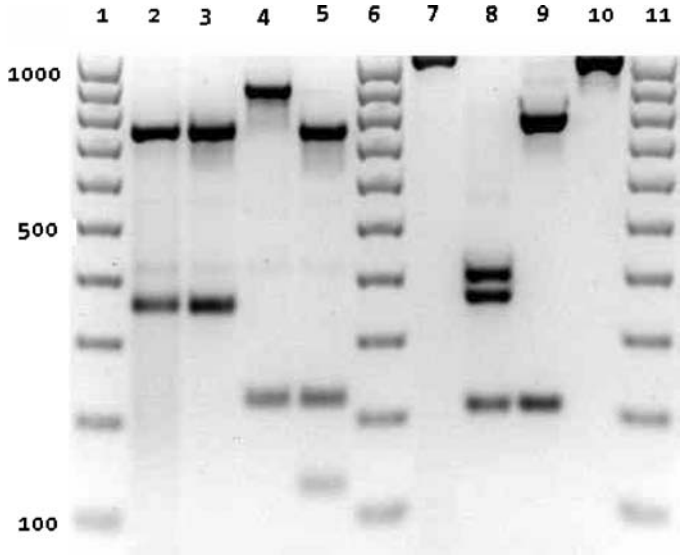

Figure 2 Mitochondrial DNA haplotypes produced after PCR amplification and digestion of the P2 and P4 mtDNA region of *Phytophthora phaseoli*, *P. infestans*, *P. ipomoeae*, and *P. mirabilis* (W.G. Flier, unpublished data). Lanes 1, 6 and 11: DNA ladder (numbers indicate size in base pairs); lanes 2 to 5, restriction fragments of amplified P2 region of *P. phaseoli*, *P. infestans* (Ia haplotype), *P. ipomoeae* and *P. mirabilis*; lanes 7 to 10, restriction fragments of amplified P4 region of *P. phaseoli*, *P. infestans* (Ia haplotype), *P. ipomoeae*, and *P. mirabilis*.

SPECIATION PATTERNS IN FOLIAR *PHYTOPHTHORA* PATHOGENS FROM MEXICO

The central highlands of Mexico, including the Toluca valley, are thought to be the center of origin and the primary center of diversity of three closely related *Phytophthora* pathogens (Figure 3). *P. infestans* and the sibling species *P. mirabilis* share a heterothallic mating system with apparently the same two mating types, A1 and A2, whereas *P. ipomoeae* has a homothallic mating system. A fourth species, *P. phaseoli*, may have originated from the central highlands of Mexico.

Host Range of *Phytophthora* Pathogens of Mexican Origin

Lesions with the appearance of late blight occur not only on potato and wild *Solanum* species, but also on *Mirabilis jalapa* L., the endemic four o'clock that is classified into the family Nyctaginaceae. *M. jalapa* is a roadside weed commonly found in central Mexico. Isolates of a *Phytophthora* species from leaf lesions on

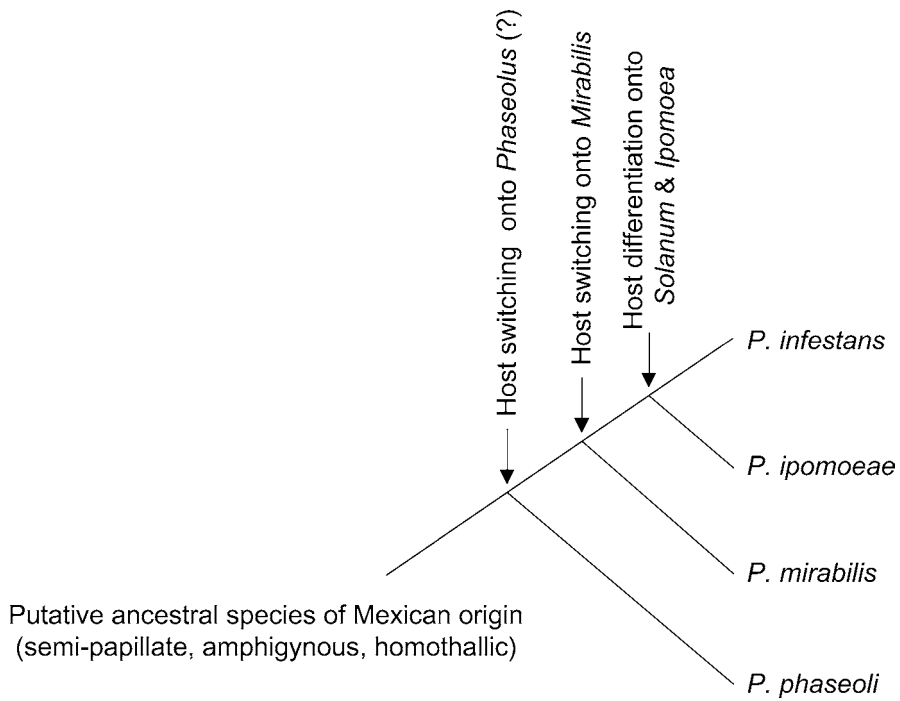

Figure 3 Coevolutionary relationships of the foliar, Mexican *Phytophthora* species related to the potato late blight pathogen *P. infestans*. This diagram represents the current consensus picture based on extensive studies on molecular systematics, host specificity, and morphology (14, 22, 29, 34, 35, 51).

M. jalapa were first considered to be *P. infestans* (71) and subsequently renamed *P. mirabilis* (29). To date, the host range of *P. mirabilis* is restricted to *M. jalapa.* Like *P. infestans*, *P. mirabilis* is amphigynous and heterothallic.

In 1998, a new *Phytophthora* species, *P. ipomoeae* Flier and Grünwald, was discovered on the native morning glory *Ipomoeae longipedunculata* belonging in the family Convolvulaceae (22). Based on morphological characteristics, ITS sequences, and other genetic markers, this new species is most closely related to *P. phaseoli, P. mirabilis*, and *P. infestans*. *P. ipomoeae* is amphigynous and homothallic (22). *P. ipomoeae* causes leaf blight symptoms with watersoaked lesions that closely resemble those of *P. infestans* and *P. mirabilis*. Recently, *I. purpurea* was reported as another host for *P. ipomoeae* in the Toluca valley (5). So far, *P. ipomoeae* has only been found in the Toluca valley in the state of Mexico (22) and the neighboring state of Michoacan (S.P. Fernández-Pavía & N.J. Grünwald, unpublished data) and is restricted to the host genus *Ipomoeae*.

Phylogeny of *P. infestans* and Related Species

Several lines of evidence point to the fact that *P. mirabilis*, *P. ipomoeae*, and *P. infestans* evolved from a common ancestor (Figure 3). Both *P. mirabilis* and *P. ipomeae* are host specific and have been found only in central Mexico. Except for heterothallism in *P. infestans* and *P. mirabilis* and homothallism in *P. ipomoeae*, these species are difficult to distinguish morphologically. Allozyme, RFLP, and AFLP analyses have shown these species to be of unique and distinguishable genotypes (22, 35). The geographic distribution of both pathogen and host plant ranges show considerable overlap (35). These differences would be expected if sympatric evolution had occured.

A recent phylogenetic analysis of the genus *Phytophthora* based on mitochondrial and nuclear DNA sequences (51) confirmed that *P. ipomoeae* is consistently placed within the Ic clade (14) with *P. infestans, P. phaseoli*, and *P. mirabilis*. *P. phaseoli* first diverged from the other members of this clade (51). Interestingly, whereas *P. infestans* and *P. mirabilis* are heterothallic, *P. ipomoeae* and *P. phaseoli* are homothallic. Based on an extensive phylogenetic analysis Kroon et al. (51) consider homothallism to be the ancestral condition in the genus *Phytophthora*, with several independent transitions to heterothallism. Kroon et al. (51) consider *P. ipomoeae* and *P. phaseoli* to be secondary homothallics.

How did these plant pathogens evolve from a common ancestral species? The three sibling species *P. infestans*, *P. mirabilis*, and *P. ipomoeae* are plant pathogens with nonoverlapping, distinct host ranges belonging to three different plant families. Native *Solanum* spp., *Mirabilis jalapa*, *Ipomoeae* spp., and *Phaseolus coccineus* all coexist in close proximity. The evolution of sibling pathogens may be driven by chance mutations or hybridization, as has been observed for other *Phytophthora* species (1, 11, 12), resulting in adaptive radiation (70). Host specialization and the trade-off in compatibility of pathogens to these hosts may define

the outcome of the evolutionary process (7, 8, 44). More experimental work is needed to test the hypothesis presented in Figure 3 that host switching followed by reproductive isolation indeed resulted in evolution and sympatric speciation in the genus *Phytophthora*. These efforts should include dating of phylogenies and identification of other extant relatives in Mexico including *P. phaseoli*.

OUTLOOK

The most parsimonious explanation for the coexistence of *P. infestans*, *P. mirabilis*, *P. ipomoeae*, and possibly *P. phaseoli* is that they arose through sympatric speciation via adaptive radiation (see Figure 3). Certainly all four hosts, namely wild potato, four o'clock, morning glory, and scarlet runner beans, exist in close proximity. All four pathogen species have a host range that is specifc to a plant family. Finally, rDNA, mitochondrial, and nuclear sequences as well as morphological characteristics all support the idea that these four *Phytophthora* species are monophyletic. It thus seems reasonable to advance the hypothesis that central Mexico is the center of evolution of *Phytophthora* clade 1 and that today's specialized *Phytophthora* pathogens are the result of sympatric evolution, driven by host switching and adaptive radiation.

Several interesting questions emerge from this hypothesis. Given the fact that many R-genes evolved in the *Solanum-P. infestans* arms race, can we expect that R-genes also coevolved in the interaction of the relatives of *P. infestans* with their respective hosts? How many potato R-genes are there? What is the phylogenetic history of these R-genes? Are hybrid progeny between these four *Phytophthora* species viable? Has hybridization played a role in speciation of these *Phytophthora* species? Are scarlet runner beans (*Phaseolus coccineus*) commonly found in the Toluca valley hosts to *P. phaseoli*? How many other endemic, related *Phytophthora* species are there? It appears that Toluca will remain a fertile ground for many future investigations.

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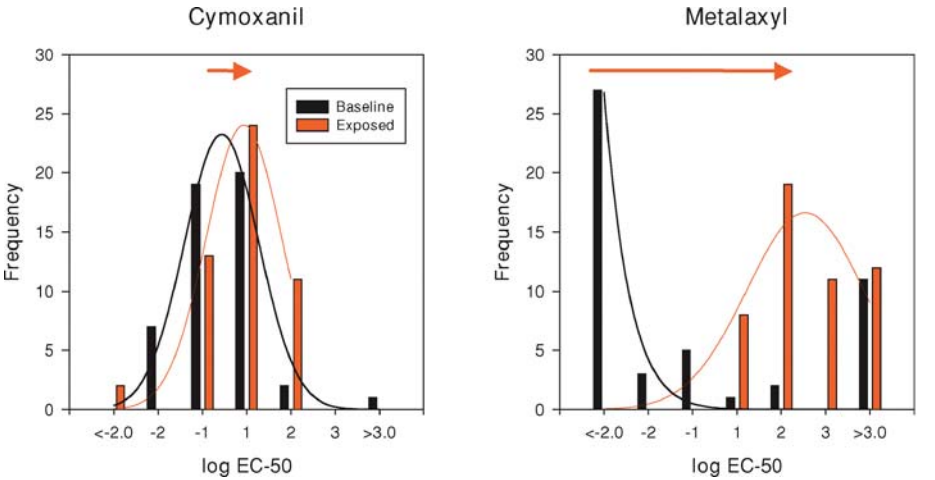

Figure 1 Distribution of the logarithm of EC-50 values before and after exposure of the population of *Phytophthora infestans* to cymoxanil or metalaxyl (N.J. Grünwald & W.E. Fry, unpublished data). Classes of sensitivity were based on the logarithm of EC-50 values and defined as follows: ≤ -2.0, > -2.0 to ≤ -1.0, > -1.0 to ≤ 0.0, > 0.0 to ≤ 1.0, > 1.0 to ≤ 2.0 and > 2.0 μg ml^{-1}. The two-sided probability values given were determined using a Monte Carlo approximation to the Fisher's exact test for s $\times$ r tables contrasting the frequency distributions for baseline and exposed populations for each fungicide. The arrows indicate the direction (and approximate magnitude) of a statistically significant shift in median from distributions before and after exposure of the population to a fungicide.

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