

## Recent developments concerning the population biology and control strategies of *Phytophthora infestans* in the USA

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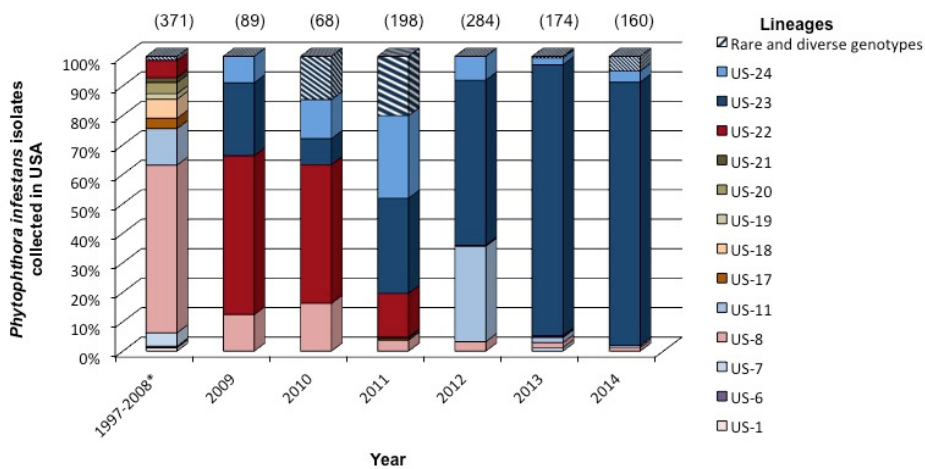
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Late blight of potato and tomato has been sporadically important in the USA. Locally, there can be important epidemics annually, but there have been only two regional pandemics in the past several decades. In 1994/1995, the introduction of the US-8 clonal lineage caused major damage in most potato growing regions of the USA (Fry and Goodwin 1997; Johnson *et al.* 1997). In 2009, widespread distribution of the US-22 clonal lineage on tomato transplants led to a pandemic that was particularly hard on home owners and organic gardeners throughout northeastern USA (Fry *et al.* 2013).

The population of *P. infestans* in the USA continues to be dominated by relatively few clonal lineages (Hu *et al.* 2012; Fry *et al.* 2013). The most recent dominant strains are US-8, US-11, US-22, US-23 and US-24 (Fry *et al.* 2015) (Fig. 1). Individuals within a lineage are very similar to each other in most characteristics. However, there are important differences among lineages (Danies *et al.* 2013; Fry *et al.* 2015). For example, the most common lineages differ in terms of their response to mefenoxam, the most effective oomycete fungicide against sensitive strains (Fry *et al.* 1979). Mefenoxam is ineffective against resistant strains (Goodwin *et al.* 1996). From the mid-1990s to 2009, most clonal lineages in the USA were resistant to mefenoxam (Fry *et al.* 2015), so growers did not use mefenoxam during the mid-1990s to 2009 to manage late blight. We discovered in 2009 that the dominant lineage (US-22) was sensitive to mefenoxam and we've subsequently learned that some lineages dominant since 2009 have also been sensitive to mefenoxam (Hu *et al.* 2012; Saville *et al.* 2015). Thus knowledge of the lineage in a particular area provides crucially important information necessary to select the most effective management strategy.

Stimulated by the 2009 pandemic and supported by a USDA AFRI grant (from March 2011 through February 2016) a group of collaborators has combined to develop near real-time information on the populations of *P. infestans* in the USA. Microsatellite markers developed by Lees *et al.* (2006) were used to identify the clonal lineage of *P. infestans* in each sample that was submitted to a central laboratory for analysis. The specimens were sent mostly by collaborators via overnight courier and in the vast majority of cases the results were returned to the submitter within one or two days of receipt. The data are also reported on a national website (USAblight.org), which also contains a map illustrating the location (county) (Fig. 2). This

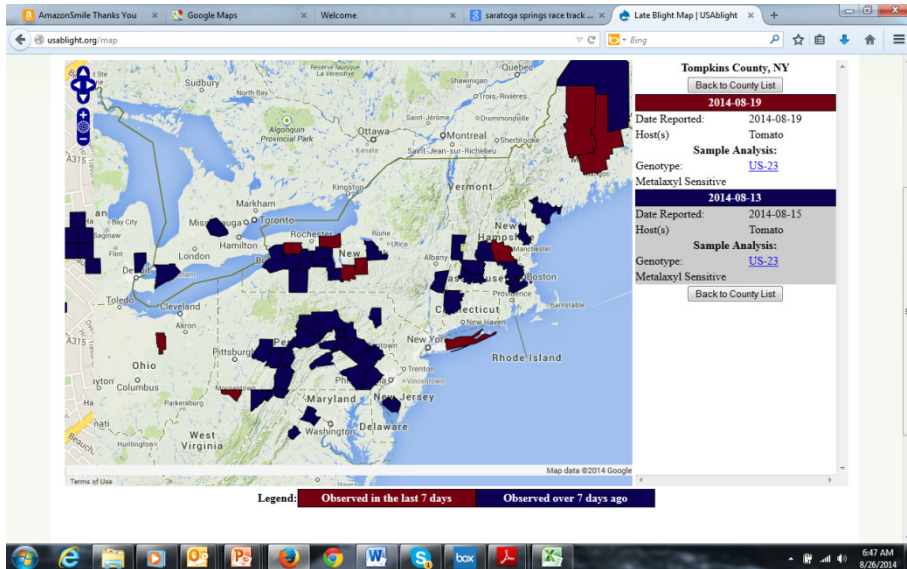
information was valuable to the submitter because each clonal lineage had reasonably consistent and unique fungicide resistance and host preference characteristics, which could help growers develop their management plans (Table 1) (Danies *et al.* 2013). During the AFRI project, use of the website increased dramatically each year, so that in 2014 alone, there were more than 25,000 visits to the website, which identified 349 active sites and more than 16,000 alerts were distributed to interested persons.



**Figure 1.** Dominant clonal lineages detected in the USA from 1997 through 2014. \* The data for 1997-2008 are from the Fry Lab; Hu *et al.* 2012; and (Wangsomboondee *et al.* 2002); the data for 2009-2014 are from the Fry lab, the Ristaino lab and the USAblight consortium. The sample size for each year is indicated in parentheses at the top of each column. (This Figure and legend are from Fry *et al.* (2015))

**Table 1.** Phenotypic characteristics of the most common clonal lineages of *Phytophthora infestans* detected in the USA 2009-2014. (Data are from Childers *et al.* 2015; Danies *et al.* 2013, and Hu *et al.* 2012)

Lineage	Mating type	Host Preference	Mefenoxam sensitivity
US-8	A2	Potato	moderately resistant
US-11	A1	Potato and Tomato	resistant
US-22	A2	Potato and Tomato	sensitive
US-23	A1	Potato and Tomato	sensitive – moderately sensitive
US-24	A1	Potato	moderately sensitive



**Figure 2.** Screen shot from USABlight.org/map from 19 August 2014. This map illustrates the reported occurrences of late blight during 2014. The most recent occurrences (in the previous 7 days) are indicated in maroon. This particular screen shot provides data for Tompkins County NY, and indicates that US-23 had been reported on 19 and 15 August 2014. The rapid identification of lineage and rapid reporting of location of late blight were crucial for precise informed management of late blight

The USABlight site also has a link to a Decision Support System (DSS) for tomato and potato late blight management (Small *et al.* 2015a). The DSS is available on the web and integrates several models into a system that can be used to predict disease dynamics based on weather conditions, host-crop resistance, and management tactics. A grower identifies the location of her/his production unit of interest (field) and the system automatically obtains observed weather data from the nearest available weather station. The system also obtains forecast weather data from the National Weather Service - National Digital Forecast Database for that specific location. The DSS uses these weather data along with crop and management information to drive disease forecasting systems (Blitecast and Simcast). A validated mechanistic model of late blight generates location-specific management recommendations for fungicide application. An integrated alert system allows users to receive notification of upcoming critical thresholds via e-mail or text message. The DSS provides producers, consultants, researchers and educators with a tool to obtain management recommendations, evaluate disease management scenarios, or explore comparative epidemiology. In field and computer simulation experiments (Small *et al.* 2015b), DSS-guided schedules were influenced by prevailing weather and host resistance and resulted in schedules that reduced the amount of fungicide used by up to 50%. In situations with weather unfavorable to disease, the DSS recommended fewer fungicide applications with no loss of disease suppression. In situations of very favorable weather, the DSS recommended more fungicide applications but with improved disease suppression. On average the DSS improved the "efficiency" of each fungicide application. ("Efficiency" = the amount of disease suppression from each fungicide application.) The DSS provides an interactive system that helps users maximize the efficiency of their crop protection strategy by enabling well-informed decisions.

Knowledge of pathogen strain(s) in an area is very beneficial to late blight management. The simplicity of the population structure has been useful to the management of late blight in the USA (Fry *et al.* 2015). This is because the phenotype of most individuals within a lineage is relatively conserved. Characterizing the phenotype of an isolate can require weeks to months – particularly if one needs to work with the isolate in pure culture. However, determining the genotype of the pathogen from a sporulating lesion using simple sequence repeats [SSRs, or microsatellites] can be done in less than 24 hours. Thus, from knowledge of the phenotype of individuals in a lineage, we can typically predict the impact of certain management actions based on genotypic analysis of the pathogen in a sample. For example if tomato growers are aware of potato late blight in the area, and if they also know that the lineage causing potato late blight is US-8 or US-24, they can safely conclude that their tomato crop is not at great immediate risk – neither US-8 nor US-24 is particularly aggressive to tomatoes. In contrast, if the lineage on potato is US-23 they need to take immediate precautions because US-23 is very aggressive on tomatoes. Growers would also know that mefenoxam could be used to help protect their tomato crop because US-23 has been largely sensitive to mefenoxam in the USA. In contrast, if US-11 was on potato, then immediate action not involving mefenoxam would be necessary because US-11 has been consistently highly pathogenic to both tomato and potato and resistant to mefenoxam (Saville *et al.* 2015). Of course it is necessary to continually monitor the phenotypes of diverse strains to learn if strains with new epidemiologically important traits have appeared.

There are several reasons that it is important to continue monitoring populations in the USA. One reason is that new lineages can become dominant. New lineages have been introduced via migration (Goodwin and Drenth 1997) and via recombination (Gavino *et al.* 2000). While populations of *P. infestans* remain strongly clonal in the USA, two recombinant populations have been described since 1990. These populations have been ephemeral because after the initial detection, there has not been further production of recombinant individuals and most strains were not detected subsequently – probably because most of the recombinants were not as fit as the dominant genotypes. The first such recombinant population was detected in the Columbia basin of the Pacific Northwest in 1993 (Gavino *et al.* 2000). The authors postulated that the parents of this population were US-6 and US-7, and that one of the progeny was US-11 (Gavino *et al.* 2000), a lineage that has been very troublesome for more than 20 years. However, other progeny of this recombination event have not been detected for many years.

The second recombinant population has been reported recently from the northeastern part of the USA (Danies *et al.* 2014). The majority of isolates were detected in central/western New York State. These isolates were detected in 2010 and 2011, but not in 2012 or 2013. As in the Pacific Northwest in 1993, this population contained diverse individuals in a somewhat localized region and had great diversity for allele combinations based on analysis of allozymes, mating type, RFLPs, and microsatellites (Danies *et al.* 2014). The parents for this population were postulated to be US-22 (A2) and at least two other genotypes. Using a recent protocol that identifies at least 36 mitochondrial haplotypes, these individuals were all determined to have the same mitochondrial haplotype (H-20), the same haplotype as US-22 (Danies *et al.* 2014). As with the 1993 population, most individuals from this 2010/2011 population have not been detected since 2011 (Danies *et al.* 2014). However, these two reports of recombinant progeny in the USA demonstrate that sexual reproduction is possible in the USA and may happen again. Because recombinants will have different phenotypes from either parent, and because there's a chance

that one of them could become a dominant lineage, it's crucial to determine the phenotypic characteristics of any recombinant individual.

**In summary**, the population of *P. infestans* in the USA remains quite simple with a few clonal lineages dominating. Currently, US-23 is most dominant. Reports of the lineage in an area enables one to develop an efficient management strategy; this is because the phenotypes of the common lineages have been determined, so it is possible to predict phenotype from knowledge of lineage. A collaboration among investigators throughout the USA assures that this information is available via a public website. A web-based DSS enables further efficiencies by using local weather data and local weather forecasts to drive two late blight forecasters.

## ACKNOWLEDGEMENTS

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