

VARIATION AND ITS ORIGINS IN *Phytophthora infestans* AND THE CONSEQUENCES FOR LATE-BLIGHT CONTROL IN POTATO AND TOMATO*

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ABSTRACT

Phenotypic markers such as mating type and genetic markers based upon biochemical and molecular polymorphisms have revealed recent major changes in the population dynamics of *Phytophthora infestans*, late-blight of potato and tomato. In all continents except Australasia both A1 and A2 mating types have been recorded. The previous A1 clonal "old" population has been displaced by "new" A1 and A2 genotypes. These appear to be of Mexican origin and were probably imported into Europe in shipments of potato tubers in the mid-1970's, and more recently on tomatoes into North America. Further migrations of new genotypes have probably occurred as a result of large scale international trade in European seed potato tubers. Sexual reproduction in late-blight populations is now possible and reported to have occurred in countries outside Mexico. Oospore ecology and epidemiology are currently being investigated in several countries. The relative importance of sexual and parasexual events need to be established in relation to crop protection strategies based upon late-blight resistant cultivars and fungicides.

RESUMEN

Mediante marcadores fenotípicos como el tipo de apareamiento y de marcadores genéticos basados en polimorfismos bioquímicos y moleculares, se han revelado cambios importantes en la dinámica poblacional de *Phytophthora infestans*, causante del tizón tardío de la papa y del tomate. En todos los continentes, excepto Australasia, se han encontrado los tipos de apareamiento A1 y A2. La población clonal "antigua" A1 previa ha sido desplazada por los "nuevos" genotipos A1 y A2. Aparentemente estos son de origen mexicano, probablemente importados en Europa en tubérculos de papa a mediados de los años 1970 y, recientemente, en tomates importados en los Estados Unidos. Migraciones de estos genotipos ocurren gracias al gran comercio internacional de tubérculos de papa europea empleada como semilla. Ahora es posible la reproducción sexual en poblaciones de tizón tardío lo cual ha ocurrido en México y otros países. La ecología y epidemiología de las esporas es sujeto de investigación en varios países. La importancia relativa de la reproducción sexual y parasexual debe establecerse en relación con las estrategias de protección vegetal basadas en cultivares resistentes al tizón tardío y el uso de fungicidas.

Mutation is the ultimate source of new variation, whilst recombination promotes the generation of novel genotypes (Burnett 1975). Late-blight of potato and tomato, caused by *Phytophthora infestans*, produces enormous numbers of multinucleate sporangia during epiphytotic. This ideally provides opportunities for new genotypes to arise by mutation as well as favouring dispersal. Dispersal leads to migration and exposure to selection. In agricultural situations selection has involved host cultivars with monogenic race-specific resistance

(R-genes in potato and Ph-genes in tomato), and site-specific systemic fungicides belonging to the phenylamide group, e.g. metalaxyl.

In natural plant communities selection imposed by resistant host genotypes has produced genetic diversity in both host and pathogen populations. Person (1966) argued that cycles of selection especially in gene centres would create the greatest diversity. For late-blight the gene centre in the central highlands of Mexico and this region is also a secondary gene centre for *Solanum* (Niederhauser 1991).

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Various studies have confirmed the pioneering work of Niederhauser (1956) and Gallegly and Galindo (1958) who described sexual reproduction in Mexico. For example, Tooley *et al.* (1985) demonstrated by allozyme analysis that Mexican populations were in expected Hardy-Weinberg equilibrium. Later studies using other selectively neutral markers based upon RG57, a highly polymorphic moderately repetitive nuclear DNA probe that hybridizes to more than 25 different loci in *P. infestans* (Goodwin *et al.* 1992a) further demonstrated the high level of genetic diversity in late-blight populations in central Mexico (Goodwin *et al.* 1992b).

These two analytical tools, allozymes and DNA fingerprinting, have been used to show that two major migrations of *P. infestans* have occurred from central Mexico. The first was in the mid-1840's leading to the Irish potato famine and the second occurred in the mid-1970's. Further migrations northwards from Mexico into the United States have recently been documented (Goodwin *et al.* 1994b). In analysing several hundred isolates from 20 countries Goodwin *et al.* (1994a) have shown that a single 'old' clonal linkage dominated populations worldwide until displacement by 'new' genotypes began after the recent second migration. The 'old' genotypes were solely A1 mating type and therefore reproduction was asexual. Rare variants among the 'old' populations for allozyme and or DNA fingerprint loci could be accounted for by mutation and/or mitotic recombination.

P. infestans is diploid (Shattock *et al.* 1986) but higher ploidy is also recognized (Whittaker *et al.* 1991). Mutation or recombination during mitosis will produce homozygous variants at heterozygous loci. Recent inheritance studies of virulence (Al-Kherb *et al.* 1995) show that in conforming to a gene-for-gene relationship with R-genes, many avirulent loci are heterozygous in wild type isolates. One step mutation or mitotic recombination would produce virulent homozygous recessive genotypes exposed to selection upon

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production of uni-nucleate zoospores. Directional selection from the planting of R-gene cultivars in the United Kingdom in the 1960's accounted for increasing frequency of complementary virulence factors 1, 2 and 3 (Malcolmson 1969). Several of the other virulence factors, namely 4-11, also were recorded at a high frequency although complementary R-genes were not present in commercial cultivars (Shattock *et al.* 1977). This may be due to linkage (Al-Kherb *et al.* 1995) or pleiotropic effects.

The second migration of late-blight isolates from Mexico occurred when tubers were imported into north-west Europe (Niederhauser 1991) because of shortages following an exceptionally dry growing season in 1976. This migratory effect was continued between European crops by epidemic spread of disease, and into different continents presumably through blighted 'seed' tubers of European origin and in tubers for consumption (Fry *et al.* 1993). As a result A2 mating types were first reported in Swiss potato crops (Hohl & Iselin 1984) and in imported Egyptian tubers for sale in the United Kingdom (Shaw *et al.* 1985). Ten years later A2 mating type isolates have been reported from all continents except Australasia.

Where 'new' genotypes of both A1 and A2 mating types have appeared they have rapidly displaced 'old' genotypes. Wild type isolates collected in 1978, 1982

Table 1. Characterization of isolates of *Phytophthora infestans* collected in North Wales, United Kingdom (1978, 1982 and 1987).

Year	isolates (No.)	mating type	allozyme Gpi	genotype Rep	mtDNA haplotype	frequency
1978	9	A1	86/100	92/100	I-b	1.0
1982	11	A1	86/100	92/100	I-b	0.45
		A1	90/100	83/100	I-a	0.18
		A2	100/100	100/100	II-a	0.18
		A1	100/100	96/96	II-a	0.09
		A1	100/100	100/100	I-a	0.09
1987	9	A1	100/100	100/100	II-a	0.33
		A2	100/100	100/100	II-a	0.22
		A1	90/100	100/100	I-a	0.11
		A2	90/100	100/100	I-a	0.11
		SF	90/100	100/100	I-a	0.11
		A1	90/100	83/100	I-a	0.11

and 1987 in North Wales were compared for mating type, allozyme loci and mitochondrial DNA haplotype (Table 1).

In addition to observing A2 mating types in 1982 the allozyme genotypes 86/100 and 92/100 at the glucosephosphate isomerase and peptidase loci respectively, had disappeared by 1987. Similarly the mitochondrial DNA haplotype type I-b (Carter *et al.* 1990) was replaced by haplotypes I-a and II-a (R. Folkertsma, R.C. Shattock and D.S. Shaw, unpublished data).

At about the same time as 'new' genotypes were beginning to establish populations in Europe, the phenylamide fungicides became commercially available. Quite rapidly phenylamide-treated crops became blighted in Ireland and other European countries (Dowley & O'Sullivan 1981; Davidse *et al.* 1981). Soon three phenotypes were recognised among field isolates; phenylamide-sensitive, insensitive and intermediate (Pappas 1985; Shattock *et al.* 1990). Inheritance studies (Shattock 1988) explained these phenotypes on the basis of a single incompletely dominant gene with intermediate phenotypes being heterozygous. The frequency of different phenotypes in blighted crops appears to depend upon fitness differences between late-blight isolates (Clayton & Shattock 1994) and the ways in which phenylamides (which can only be used as prepacked mixtures with non-systemic fungicides) are used during the growing season (Davidse *et al.* 1989). Directional selection for phenylamide-insensitive phenotypes, as in the case with virulence for certain R-genes in potato cultivars, has produced a "boom-and-bust" situation. However, because fungicides can be used flexibly within a season phenylamides can still be used as long as highly pathogenic phenylamide-insensitive phenotypes are not predominant.

Until recently phenylamides remained effective in the USA where 'old' genotypes have persisted. The situation, however, is changing. Genetically diverse isolates, thought to have spread directly from north-west Mexico on tomato (Goodwin *et al.* 1994b), have begun to cause serious late-blight attacks on potatoes and tomatoes in various states (Goodwin and Fry 1994). Some

of these isolates are resistant to phenylamides as are many in Mexico both on treated crops and untreated wild hosts (Matuszak *et al.* 1994).

The changing population dynamics of *P. infestans* over the past two decades has produced new problems worldwide. Not least is the occurrence of both mating types with the real threat of soil-borne inoculum (oospores) giving rise to recombinant progeny capable of initiating earlier outbreaks of late-blight (Drenth *et al.* 1995).

Attention is now shifting to discover whether or not novel variants are arising from sexual reproduction in those countries, other than Mexico, where both A1 and A2 mating types have been found. So far evidence for sexual recombinations has been inferred from studies in Poland (Sujkowski *et al.* 1994) and The Netherlands (Drenth *et al.* 1994). Detailed and extensive sampling is required to determine temporal and spatial allelic frequencies. For this to be achieved a large number of codominant markers are necessary such as allozymes and single copy nuclear DNA restriction fragment length polymorphisms (RFLP's) (Carter *et al.* 1991). So far, relatively few have been identified and unfortunately the abundant markers based upon random amplified polymorphic DNA (RAPD's) (Judelson *et al.* 1994) are not co-dominant and not directly useful except for haploid pathogens such as powdery mildews (Wolfe and McDermott 1994).

Whilst the emergence of new populations of late-blight highlights problems for potato crops (Van der Zaag 1994) tomatoes are also severely affected by *P. infestans*. Host specialization has often been described and recently, as new genotypes have appeared in the USA, Legrand and Fry (1995) have compared the pathogenicity of so called tomato-adapted and tomato-unadapted types. The former attack both potato and tomato whilst the latter only seriously affect

potato. To ascertain the genetic basis of aggressiveness to different hosts Yun Lee and Fry (1994) have begun to analyse sexual progeny of parental isolates conforming to tomato-adapted and unadapted phenotypes.

In countries where both potatoes and tomatoes are cultivated it has been observed that

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tomatoes do not always become affected by *P. infestans* when adjacent to blighted potatoes (Egypt, D.S. Shaw, personal communication). In Costa Rica where tomatoes and potatoes are spatially separated, for example in the Cartago region, sampling may reveal that host-specific phenotypes exist with different population structure for selectable and non-selectable traits.

All isolates from Costa Rica have been shown to be A1 mating type (Hohl & Iselin 1984; Goodwin *et al.* 1994; Vera Sanchez-Garita, CATIE, Costa Rica pers. comm.) and haplotype I-a for mitochondrial DNA (G.W. Griffith, unpublished data). Some are also insensitive to phenylamides. Goodwin *et al.*, (1994) did not classify eight Costa Rica isolates collected in 1982 and 1993 as either 'old' or 'new' because they were all a previously undetected genotype (94/94) at the peptidase locus. However, the evidence of type I-a mitochondrial DNA indicates that the isolates are not 'old' but neither are they necessarily part of the 'new' population arising from the second migratory event of the 1970's.

The proximity to the gene centre in central Mexico may indicate separate southerly migrations to Central American countries equivalent to the current northerly ones into the USA. Integrating cultural practices, resistant cultivars and crop protection chemicals are necessary to combat late-blight. Breeders are working to produce cultivars with polygenic late-blight resistance (Wastie 1991), that will be durable (Turkensteen 1993). To assist this aim it is important to remove monogenic (R-gene) resistance from breeding lines. Failure to spot R10 in the pedigree of Brodick, which was promoted as a race non-specific resistant cultivar (Wastie 1991), produced poorer than expected performance in trials and commercial plantings.

New chemistry is awaited to produce systemic and curative fungicides to match the early promise of the phenylamides. Meanwhile the usefulness of the range of available protectant, e.g. mancozeb, fluazinam, and translaminar products, e.g. cymoxanil, dimethomorph, propamocarb may be affected by forthcoming environmentally led statutory, rather than voluntary, reduction in fungicide-usage proposed in

certain countries (Oloffson 1991). A century and a half after the Irish potato famine biotechnology based upon DNA technology and manipulation of genes outside living cells is revolutionising biological and agricultural research. Gene mapping is underway in both *P. infestans* (Judelson *et al.* 1994) and the potato and tomato (Tanksley *et al.* 1992).

As various plant resistance genes are located, cloned and characterised (Knogge 1994) there is an expectation of the emergence of more effective resistant genotypes to plant diseases. Both race-specific and race- non specific late-blight resistance factors have been mapped (Gebhardt 1994). Other techniques have produced fusion hybrids between potato and tomato opening up the possibility of genomic transfer between both hosts (Jacobsen *et al.* 1994). These and

other advances e.g. (de Wit 1992; Strittmatter & Wegener 1993) may lead to transgenic plants which exhibit novel forms of durable non race-specific resistance.

The relative importance of sexual and parasexual events need to be established in relation to crop protection strategies based upon late-blight resistant cultivars and fungicides.

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