J. Mycopathol, Res, ***46(2)*** *: 163-183(2008)*

Progress in research on *Phytophthora* : Identification, species diversity and population diversity

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This review article discusses the various recent molecular methods used in the identification of the *Phytophthora* species, their limitations and the current revised picture of species diversity emerging worldwide as a result of the use of these techniques. The phenotypic and genotypic diversity of these phytopathogens worldwide have been inferred with the use of both molecular and morphological markers.

Key words: rDNA-ITS region, coding regions, dominant and co-dominant markers, population structure.

IDENTIFICATION AND SPECIES DIVERSITY OF *PHYTOPHTHORA*

The taxonomy of the genus *Phytophthora* is based mainly on morphological and growth characteristics encompassing sporangial structures, antheridial forms, host specificity and breeding systems (Tucker, 1931; Waterhouse, 1963; 1970; Newhook *et al.*, 1978; Ho, 1981; Stamps *et al.*, 1990). Unfortunately many of the characteristics used so far for species identification are plastic, highly influenced by environment, and show transgression between species having an unknown genetic basis (Drenth and Sendall, 2004b). Furthermore, taxonomic problems arise from the assignment of a "type isolate" (*c.f.* Leonian, 1934; Hansen, 1991; Brasier, 1992) to act as the exemplar for descriptions of the species, whose selection itself might have been 'fortuitous' in the first place, and as such cannot conceivably represent the intraspecific variability of an entire population nor it is likely to represent the mean of this variability (Brasier, 1991). Moreover, in light of growing evidence from molecular and ecological studies it has become apparent that taxonomic grouping based solely on morphological criteria might be artificial (Gallegly 1983; Brasier, 1991; Brasier and Hansen, 1992); in addition, there are species which do not produce asexual and/or sexual structures in culture media, or sometimes even in host plants (Erwin and Riberio, 1996); in other species, induction of reproductive structures requires subtle manipulations of nutritional and environmental factors. Diagnosis based on phenotypic characters has also proven to be insufficient when intraspecific variations in reproductive and other traits are great, and often phenotypic similarities may occur among species coexisting in the same habitat. The increasing presence of species hybrids compounds the problem, as they are less likely to be recognized by conventional approaches (Brasier, 2000; Olson and Stenlid, 2002; Schardl and Craren, 2003). In spite of these limitations some morphological parameters like pedicel length and length/breadth ratio can continue to play a role in identification (Appiah *et al.*, 2003).

In the last three decades, in addition to morphological approaches various attempts have been made to use other methods to simplify and improve the accuracy of identification of isolates to a species level, including use of protein patterns (Hansen *et al.*, 1986; Bielenin *et al.*, 1988), isozymes (Nygaard *et al.*, 1989; Mills *et al.*, 1991; Oudemans

and Coffey, 1991a; b; Mchau and Coffey, 1994; Oudemans *et al.*, 1994; Mchau and Coffey, 1995), serology (Jones and Shew, 1988; McDonald *et al.*, 1990; Benson, 1991; Cahill and Hardham, 1994; Robold and Hardham, 1998; Gautam *et al.*, 1999; Grote and Gabler, 1999; Ferraris *et al.*, 2004), RFLP analysis of nuclear and mitochondrial DNA (Förster, and Coffey, 1991; Förster and Coffey, 1993; Möler *et al.*, 1993; Lacourt *et al.*, 1994; Tooley *et al.*, 1996; Cooke and Duncan,1997, Förster *et al.*, 1998; Ristaino *et al.*, 1998; Hong *et al.*, 1999a; Chowdappa *et al.*, 2003a; Martin and Tooley, 2004a, b) and more recently SSCP analysis of the ITS region of rDNA (Scott *et al.*, 1988; Kong *et al.*, 2003a; 2004).

Species specific probes and primers based on (i) DNA probes [*P. parasitica* (Goodwin *et al.*, 1989; 1990a), *P. citrophthora* (Goodwin *et al.*, 1990b), *P. cinnamomi* (Judelson and Routh, 1996)], (ii) PCR of random sequences [*P. parasitica* and *P. citrophthora* (Ersek *et al.*, 1994), *P. infestans* (Niepold and Schober-Butin, 1995), *Phytophthora* isolates from Alder (DeMerlier *et al.*, 2005)], (iii) PCR of DNA of ITS region [*P. capsici*, *P. cinnamomi*, *P. megakarya* and *P. palmivora* (Lee *et al.*, 1993), *P. cambivora*, *P. quercina*, *P. citricola* (Schubert *et al.*, 1999), *P. capsici*, *P. citricola*, *P. citrophthora* (Ristanio *et al.*, 1998), *P. infestans*, *P. erythroseptica*, *P. nicotianae* (Tooley *et al.*, 1997), *P. nicotianae* (Grote *et al.*, 2002), *P. nicotianae* and *P. citrophthora* (Ippolito *et al.*, 2004), *P. capsici* (Silvar *et al.*, 2005)], (iv) PCR of other genes or spacers: (a) intergenic region between 5S and small ribosomal subunit – *P. medicaginis* (Liew *et al.*, 1998), (b) *ParA1* elicitin gene sequence – *P. nicotianae* (Lacourt and Duncan, 1997; Kong *et al.*, 2003b), (c) storage protein genes – *P. cinnamomi* (Kong *et al.*, 2003c), and (d) mitochondrial *cox* I and II genes – *P . ramorum*, *P. nemrosa*, *P. pseudosyringae* (Martin *et al.*, 2004), (v) PCR amplification and differentiating of the amplicons by electrophoresis (Maes *et al.*, 1998), (vi) PCR amplification and differentiating of the amplicons by hybridization [*P. cinnamomi* (Dobrowolski and O'Brien, 1993)]as well as for identifying hybrids (Bakonnyi *et al.*, 2006) have proven useful in Phytophthora disease diagnosis because of their high levels of sensitivity and generally high specificity for accurate identification.

Some DNA based methods are advantageous because pathogen isolation is not required and PCR amplification can be performed directly from DNA extracted from the infected tissue. DNA sequence data obtained in phylogenetic studies have also been used to differentiate *Phytophthora* species. Specific regions that have been examined include the large and small subunits of the rRNA (Briard *et al.*, 1995; Van de Peer *et al.*, 1996) and the ITS regions of the rDNA (Förster *et al.*, 1990; Crawford *et al.*, 1996; Cooke and Duncan, 1997; Cooke *et al.*, 2000b; Förster *et al.*, 2000, Kondo *et al.*, 2005).

While the use of protein patterns and isozymes was a major shift towards a more phylogenetic system and changed our concept of classifying *Phytophthora*, it could not account for all the intraspecific variations and suffered from the setback of complexity in case of total protein patterns. Even though isozyme banding patterns are less complex than total protein patterns and are easier to differentiate and interpret (Nygaard *et al.*, 1989), the use of isozymes for identification depends on the successful selection of the enzymes which is often important for separation of even a few *Phytophthora* species. Added to it is the cumbersome use of different buffer systems for the visualization of patterns. Though dipstick assays or ELISA were developed for *P. cinnamomi* (Hardham and Cahill, 1993; Gabor *et al.*, 1993; Cahill and Hardham, 1994), only polyclonal antisera are available commercially (Benson, 1991). Moreover, the A379II antibody (Ferraris *et al.*, 2004) has the limited ability of distinguishing *Phytophthora* species only on Chestnut. Lack of specificity of some antibodies and the necessity of obtaining monoclonal antibodies complicate the use of serological techniques (Bonants *et al.*, 1997).

On the other hand, not only could nucleic acid based targets account for the variation present but was also generally more comprehensive covering most species. Sequence analysis of rDNA genes is effective but expensive even after the fall in prices of commercial sequencing, whereas mitochondrial or nuclear DNA polymorphisms or fingerprinting using RFLP is less expensive, more direct and therefore most frequently used. PCR amplification of nuclear rDNA ITS regions and its RFLP method of Cooke *et*

al., (2000a, b) is the most comprehensive till date (Martin and Tooley, 2003), but still suffers from some short comings in resolving the genetic differences of very closely related species (Tooley *et al.*, 1996; Cooke and Duncan, 1997; Ristanio *et al.*, 1998) and also as in the case of *P. ramorum*, cannot distinguish between isolates from Europe and US (Kroon *et al.*, 2004), whereas mtDNA PCR–RFLP of *cox* I and II genes (Martin and Tooley, 2004a) could distinguish these same species. Thirty one species can be distinguished consistently (Martin and Tooley, 2004b) by this method and more are being evaluated, but, the mtDNA-based system has one potential shortcoming; as the mitochondrial genes are uniparentally inherited, it cannot be used for identification and detection of interspecific hybrids. A possible complication in the use of ITS regions is the possibility of multiple forms of target sequence present in single isolates resulting in summation of RFLP band sizes of some isolates to be greater than initial amplicon size, indicating that at least 2 forms of the ITS regions were present (Cooke and Duncan, 1997; Brasier *et al.*, 2003a).

The SSCP method developed by Kong *et al.* (2003a; 2004) for *Phytophthora* can at present distinguish 30 species, its subgroups and species complex and therefore superior in many aspects than the ITS or the *cox* gene based systems, but detection of hybrid species have not yet been tested. Presently, emphasis is being given on to develop a comprehensive SSCP based key to the species of *Phytophthora* (Dr. C. X. Hong, Virginia State University, USA, personal communication).

In the last two decades phylogenetic analysis of both *Phytophthora* and *Pythium* through protein patterns, isozymes and RFLPs of both mitochondrial and nuclear DNA has successfully resolved many taxonomic issues within groups of species and has also demonstrated that traditional taxonomic concepts in *Phytophthora* bear little relationship to the evolutionary structure of the genus (Brasier, 1991; Hansen, 1991; Brasier and Hansen, 1992). Cladistically many individual taxa have been further clarified by grouping them into 8 clades by the ITS based methods of Cooke *et al.* (2000b). Some of the diversification that has been generated due to the use of molecular techniques are *P. tentaculata*, *P. multivesiculata* and *P. quercina* as unique and separate species; conspecificity of *P. citricola* and *P. inflata* as well as of *P. melonis* and *P. sinensis*; separation of the traditional '*P. megasperma*' morphospecies into *P. megasperma sensu stricto*, *P. sojae*, *P. medicaginis* and *P. trifolii* (Cooke *et al.*, 2000b), *P. inundata* (Brasier, 2003b); separation of *P. drechsleri* and *P. cryptogea* (Cooke *et al.*, 2000b); reclassification of the initially identified eight isolates from various hosts in North America on the basis of isozymes & mtDNA as *P. cryptogea* / *P. drechsleri* J group of Mills *et al.* (1991) to *P. gonapodyides* (Brasier *et al.*, 2003a); subsequent validation of the separation of *P.capsici* into *P. capsici* and *P. tropicalis* (Zhang *et al.*, 2004) etc.

Added to this milieu of reclassification there has been a proliferation in the discovery of occurrences of new species [*P. ramorum* in US, sudden oak diseases (Rizzo *et al.*, 2002) and on ornamental plants in Europe (Werres *et al.*, 2001), *P. nemrosa* (Hansen *et al.*, 2003), *P. quercina* (Jung *et al.*, 1999; Cooke *et al.*, 2005), *P. ipomoeae* (Flier *et al.*, 2002), *P. glovera* (Shew and Olivera, 1998), *P. bisheria*, *P. kelmania* (Abad *et al.*, 2002), *P. europaea*, *P. psychrophila*, *P. uglinosa* (Jung *et al.*, 2000), *P. pseudosyringae* (Jung *et al.*, 2003), *P. kernoviae* (Brasier *et al.*, 2005), *P. inundata* sp. *nov* (Brasier *et al.*, 2003b), *P. captiosa* sp. nov and *P. fallax* sp. nov.(Dick *et al.*, 2006) and other unique yet unnamed taxa (Brasier *et al.*, 2003a)] and numerous natural interspecific hybrids (Man in't Veld *et al.*, 1998; Brasier *et al.*, 1999; Bonants *et al.*, 2000; Brasier *et al.*, 2000; Olson *et al.*, 2002; Brasier *et al.*, 2004; Ioos *et al.*, 2006).

In view of the above rather rapid and seminal developments, there is an urgent need to revalidate all previous reports based on morphology and also all *Phytophthora* cultures of uncertain taxonomic status deposited in collections mostly on the basis of phenotypic characterization, as unambiguous reports are not only necessary for disease control but also for clear scientific communication. Thus there has been an increase in the number of reports worldwide on molecular validation, which has not only resulted in cataloguing unambiguously for the future and bringing forth a clear picture of the diversity of species present in a region but

also has subsequently resulted in the correction of the identity of the causal organism from earlier morphological based reports, where often, new species have been wrongly assigned to current taxa and conversely, morphological variants of existing taxa incorrectly assigned as new disease threats.

In Southern Italy, reexamination by Ippolito *et al.* (2005) of all morphologically characterized disease reports has yielded new information about the presence of *P. tentaculata* (which was previously identified only as *Phytophthora* sp.) and blight of zucchini caused by *P. capsici*. In Korea species diversity was assessed on the basis of PCR–RFLP of the ITS region and small subunit of rDNA (Hong *et al.*, 1998; 1999a, b) and sequence analysis of the ITS region which showed that 16 species were present, but there were some problems of clear delimitation and identification regarding the non-papillate species. While earlier morphologically identified isolates of *P. erythroseptica* were reported to be misidentified, another isolate previously identified as *P. megasperma* was found to be closely related to *P. erythroseptica*, *P. megasperma* from chick pea and *P. cryptogea-P. drechsleri* complex and hence could not be conclusively identified (Hong *et al.*, 2000).

Besides assessing the region/country specific species diversity, species diversity in individual crops has also been studied. In cocoa, an important cash crop, molecular analysis using ITS- RFLP and ITS rRNA gene sequence was used to assess both intra and inter species diversity (Appiah *et al.*, 2004), which showed that there were 4 main cocoa associated species forming 2 distinct groups, one forming *P. capsici* and *P. cinnamomi*, and the other *P. palmivora* and *P. megakarya* and that the *P. katsurae* from earlier morphological reports was actually *P. capsici*; furthermore, it was suggested that *P. capsici* isolates may be closely related to *P. tropicalis*. Similarly *Phytophthora* species associated with ink disease of chestnut were also evaluated by ITS based methods, whereby it was seen that *P. cambivora* and *P. cinnamomi* were the causal organisms (Gouveia *et al.*, 2005). Also in another ITS based study (Yamak *et al.*, 2002) nine phylogenetically distinct taxa were found from irrigation water pathogenic to pear in Washington State area.

Mirabolfathy *et al.* (2001) using ITS–RFLP and sequencing of ITS region reported from Iran that the causal organisms for gummosis of pistachio trees are *P. melonis* and *P. pistaciae* and not *P. drechsleri* and *P. megasperma* as previously identified. Besides the diversity aspect, this had important implications for control as pistachio were grown in close proximity with cucurbits, which was known (from China and Japan) to be a host for *P. melonis*. Moreover, many of the novel species reported [like *P. kernoviae* etc. in U.K, the standard (*P. alni* subsp. *alni*) and variant (*P. alni* sub sp. *uniformis* and *P. alni* sub sp. *multiformis*) groups of *P. alni* in Europe, *P. ramorum* in US, etc.] and species hybrids as mentioned earlier are the result of renewed surveys based on this trend.

Clearer species delimitation because of ITS based methods have recently also resulted in first disease reports from regions hitherto unknown for presence of the organism or of the host association with the organism [Basal canker of Beech in Italy caused by *P. pseudosyringae* (Motta *et al.*, 2003); leaf and bract blight of *Anthurium* in Brazil caused by *P. citrophthora* (Paim *et al.*, 2006); root rot of Scotch broom in Italy caused by *P. megasperma* (Vettraino and Vannini, 2003); crown rot of red robin plant in Italy caused by *P. cactorum* (Vettraino *et al.*, 2006); *P. nicotianae* on jojoba in Argentina (Lucero *et al.*, 2005) etc].

In India few reports on molecular validation from plantation crops (Chowdappa *et al.*, 2003a, b; Tripathi *et al.*, 2003) are there, but this is grossly inadequate as about a third of the total established species of *Phytophthora* known so far has been reported from India alone mostly from plantation crops, fruits and vegetables. Moreover, some of the earlier Indian reports based solely on morphology has also not been accepted worldwide (Mehrotra and Aggarwal, 2001). Therefore, there is an urgent need for a molecular validation of the earlier morphological Indian reports.

Among vegetable crops, the causal organism *P. melonis*, of fruit and vine rot of pointed gourd was

shown by Guha Roy *et al.*, (2006) based on ITS-RFLP and sequencing of ITS region to be previously wrongly identified as *P. cinnamomi* as earlier it was based on morphology alone. The earlier report (Khatua *et al.*, 1981) was incidentally a first report of *P. cinnamomi* causing fruit and vine rot from India! Similarly, among plantation crops, the identity of *Phytophthora* associated with areca nut was found to be *P. meadii* (Chowdappa *et al.*, 2003b) and not *P. arecae* as previously thought. Molecular discrimination of *P. capsici* isolates on cocoa and black pepper and lack of differentiation of *P. palmivora* isolates between coconut and cocoa was also shown (Chowdappa *et al.*, 2003c). The identity of *P. nicotianae* as a causal organism of leaf rot of betelvine was also corroborated (Tripathi *et al.*, 2003) using ITS-RFLP based studies. Very recently a more deep characterization of Indian *Phytophthora* isolates is available in the GenBank using translational elongation factor1 alpa gene (DQ861430, DQ861432, DQ861433, DQ861434) and beta tubulin gene(DQ861435, DQ861436) both submitted by Singh, H. B. and Kumar, A from NBRI, Lucknow, India. A re examination of the *Phytophthora* species through ITS-RFLP and sequencing affecting ten economic crops and fruits were undertaken in eastern India which showed that *P. palmivora* is not a pathogen of betelvine as earlier reported, but only *P. capsici* and *P. nicotianae*. It also reported *P. palmivora* on papaya, *P. nicotianae* on black pepper and *P. capsici* on chilli for the first time from this part of the country and the ITS sequences of respective *Phytophthora* sps. were also submitted in the GenBank (Guha Roy *et al.*, 2007c; 2008). As most of the disease reports on vegetables and fruits have not been assessed in India, there is much scope left for assessing the species diversity and validating all the earlier morphological reports.

POPULATION DIVERSITY

There has been an increasing realization that more knowledge about the genetic structures of plant pathogens is needed to implement effective control strategies and this has led plant pathologists to take a population approach towards study of pathogens in the last two decades. The limits for meaningful polymorphisms having being reached, for phenotypic markers, along with the fact that there have been rapid advances in technology, molecular markers are being increasingly used worldwide for studies of diversity of pathogen populations because they fulfill relatively many of the criteria as outlined in Cooke and Lees, (2004).

In *Phytophthora* species, there being relatively few morphological characters by which to detect intraspecific variation (and in some cases even interspecific variation!), markers based on phenotype now play an accessory role as many are under polygenic control and cannot be used for inheritance studies (e.g. sporangial dimensions especially length/breadth ratio, *in vitro* growth rate on different media, mating type, virulence and some tested on limited scale like aggressiveness, temperature responses), however, a few are also under simple genetic control (e.g. sensitivity to fungicides). Detection of diversity is usually done through use of phenotypic and genotypic markers that are selectively neutral, highly informative, reproducible and relatively easy and inexpensive to assay. It is clear however, that no single marker system would be adequate for all aspects of research on diversity of *Phytophthora* species (Milbourne *et al.*, 1997). The choice of genetic marker can have a substantial impact on the analysis and interpretation of data. As *Phytophthora* reproduce mainly asexually, producing a population structure that is largely composed of clonal lineages, a neutral marker such as a DNA fingerprint may be used to address both questions relating to roles played by population size, mating systems and gene flow, and also for questions relating to effects of selections, for which usually selective markers are used; assuming there is complete correspondence between genotype (DNA fingerprint) and phenotype (for *e.g.* pathotype) (McDonald, 1997). However, such assumption may not be valid as variable pathotypes can arise within the same clonal lineages (Drenth *et al.*, 1996; Goodwin *et al*, 1995b; Abu-El Samen *et al.*, 2003).

Though it is best to use a widest practical array of genetic markers, combining a mixture of selected and neutral unlinked markers encompassing the nuclear (and mitochondrial) genome(s) distributed across many chromosomes; the number of marker loci assayed varies with the objective and resources

available to the investigator. The different types of non-DNA (allozymes) and DNA based (nuclear/ mitochondrial genome RFLP, RAPD, AFLP, ISSR, SSR and SNP) marker technologies used for analysis of diversity in *Phytophthora* species, and their relative advantages as well as shortcomings have been reviewed (Duncan *et al.*, 1998; Cooke and Lees, 2004).

Both less reliable phenotypic markers like mating type (Gallegly and Galinde, 1957), virulence (Malcomson and Black, 1966), fungicide resistance (Dowly and O'Sullivan, 1981), aggressiveness (Day and Shattock, 1997; Kato *et al.*, 1997), antibiotic resistance (Shattock and Shaw, 1975) and temperature responses (Mizubuti and Fry, 1988), and increasingly used more reliable genotypic markers like (a) codominant: isozymes (Old *et al.*, 1984; Tooley *et al.*, 1985; Nygaard *et al.*, 1989), single locus RFLPs (Carter *et al.*, 1999), 'locus-specific' SSRs / microsatellite (Knapova *et al.*, 2001; Knapova and Gisi, 2002; Cooke *et al.*, 2006), (b) dominant : moderately repetitive multilocus RFLP probe RG57 (Goodwin *et al.*, 1992b), RAPDs (Meng, 1999; Ning and Xiu-guo, 2001; Lebot *et al.*, 2003), ISSRs (Tian and Babadoost, 2003), AFLPs (Knapova and Gisi, 2002; Flier *et al.*, 2003; Cooke *et al.*, 2003; Tian and Babadoost, 2003; Chowdappa *et al.*, 2003c), and (c) others like SNP (Cooke and Lees, 2004; Lievens *et al.*, 2006) and sequence analysis (Cooke *et al.*, 2000b) have been used to assess population diversity within *Phytophthora* species; but such studies till date have by and large been confined to *P. infestans* as much of the international resources and effort GILB (Global initiative on late blight) and EU funded 'Concerted Action project', EUCABLIGHT (www.eucablight.org) are on the 'late blight pathogen'.

Studies on the phenotypic and genotypic diversity of *Phytophthora* have largely been confined to *P. infestans*, as mentioned before and understandably so! Whatever be its origin, the central highlands of Mexico (Niederhauser, 1991), or the South American Andes, which has also been proposed (Abad & Abad, 1997); before the 1970s, European populations of this pathogen appear to have consisted exclusively of a single clonal lineage of the A1 mating type, known as US–1, which had the mitochondrial DNA (mtDNA) haplotype Ib, an allozyme genotype [based on glucose-6-phosphate isomerase (*Gpi*) and peptidase (*Pep*) allozyme loci], *Gpi 86/100*, *Pep 92/100* and a characteristic fingerprint based on the moderately repetitive multilocus RFLP probe RG57 (Goodwin *et al.*, 1994b). In recent years, analyses of *P. infestans* isolates from many European countries have generally failed to detect this 'old' clonal lineage of *P. infestans*, and have shown the presence of more diverse, new populations, often containing both A1 and A2 mating type strains, with increased metalyxl resistance (Dowley and O'Sullivan, 1981) and a broader range of virulence factors (Deahl *et al.*, 1991).

There have been numerous studies worldwide using both phenotypic and genotypic markers. Within UK; diversity assessment was done on the basis of mating type, mitochondrial and nuclear (multilocus RG 57 probe) RFLP and sensitivity to the phenylamide fungicide metalayxl in Scotland, England, Wales (Day *et al.*, 2004), Republic of Ireland (Griffin *et al.*, 2002) along with RAPD in Northern Ireland (Carlisle *et al.*, 2001) and additionally by AFLP fingerprints in Scotland (Cooke *et al.*, 2003.). The A2 mating type was not detected till 1995-1996 in Northern Ireland but thereafter (Carlisle *et al.*, 2001) with low population diversity (monomorphic for *Gpi* & *Pep* loci), especially of A2 and were distinct from Great Britain and European mainland isolates. Metalayxl resistant isolates were always of A1 mating type in Britain and Scotland (Day *et al.*, 2004) and like in Ireland were found in a single AFLP group (Cooke *et al.*, 2003). Overall the presence of mixed mating type, an increasing frequency of isolates of intermediate metalayxl resistance and AFLP diversity suggest occasional sexual recombination (Cooke *et al.*, 2003) but it does not appear to be a factor in disease epimediology (Griffin *et al.*, 2002). Recent studies by Cooke *et al.* (2006), which detected new mtDNA haplotypes in Northern Ireland, have concluded similarly.

Within continental Europe: in Belgium, diversity was assessed mostly phenotypically (Heremans and Haesaert, 2004) with *in vitro* growth rate, sensitivity to fungicide metalayxl, mating type, allozyme *Gpi* & *Pep* loci and also with RFLP using RG 57 probe

which showed that A2 isolates were very low in number and the population could be characterized in 15 multilocus genotypes with some having never being previously reported in continental Europe (Bakonyi *et al.*, 2002a); in Hungary, similar phenotypic and RG 57 RFLP studies (Bakonyi *et al.*, 2002b) showed designation of 20 multilocus genotypes with the most common peptidase allele being 96 and presence of a unique 83/96 genotype, and both Belgian and Hungarian data suggesting migration and/or asexual reproduction playing a role in the recent evolution of the pathogen (Bakonyi *et al.*, 2002b; a); in Poland, phenotypic structure of the population was characterized with respect to virulence, race diversity, aggressiveness and mating type (Zarzycka *et al.*, 2001; Zarzycka *et al.*, 2002) and also genotypic diversity (Sujkowski *et al.*, 1996; Sujkowski *et al.*, 1994) indicating the appearance of new genotypes of A2 mating type in 1988 and subsequent possible occurrence of sexual reproduction (Sujkowski *et al.*, 1994), with consequent occurrence of very complex *P. infestans* pathotypes (Zarzycka *et al.*, 2001) accompanied with an increase in race diversity during 1996-2001 (Zarzycka *et al.*, 2002); in France too, phenotypic [mating type, allozyme *Gpi* & *Pep*, virulence(Andrivon *et al.*, 1994a), race structure (Andrivon, 1994b)]and genotypic diversity studies detected A2 mating type after 1995 and other characteristics which were similar to the European populations introduced after 1970, the exceptions being Southern France isolates. Overall *P. infestans* population on tomato and potato were largely separated. No geographical substructure was apparent in the races leading to the conclusion of limited gene flow in the population. In the Nordic countries of Norway and Finland, studies (Brurberg *et al.*, 1999) based on mating type and RG57 fingerprints showed the isolates from these countries were similar in terms of genotypic diversity and genetic distance between genotypes. Out of the 76 multilocus genotypes identified, 53 were unique indicating that sexual reproduction is contributing significantly to the genetic variation in Norway and Finland. In a comparative study (Knapova and Gisi, 2002) of potato and tomato isolates from Sweden, France and other European countries, using phenotypic (mating type, sensitivity to phenylamide fungicides, virulence on potato differentials and pathogenic fitness) and genotypic markers (mitochondrial DNA haplotypes, AFLP and SSR); it was found that, of the four haplotypes Ia, dominated the population (93%), 15 & 11 SSR genotypes which were never present before in potato and tomato isolates respectively and 40 AFLP genotypes were distinguishable among the isolates which suggest that the field population in Europe may have evolved from local process including sexual recombination, host preference and selection rather than through by distance migration.

In Russia, the Northern Caucasus and the Far East results from metalayxl sensitivity, mating type, allozyme *Gpi*, *Pep* and *Me* (Elansky *et al.*, 1999a; b) virulence genes and compatibility type (Vedenyapina *et al.*, 2002), oospore occurrence (Amatkhanova *et al.*, 2004), mt DNA haplotype and nuclear RG57 RFLP (Elansky *et al.*, 2001) showed higher levels of inter-population diversity from potato and tomato than intra-population diversity with asexual reproduction predominating in the field (Elansky *et al.*, 1999a). Population diversity near Moscow was highly diverse with 15 unique genotypes in contrast to Siberia, which had limited diversity in which a dominant clonal lineage SIB-1 was found (Elansky *et al.*, 2001).

South American countries are at the *P. infestans*'s host's center of diversity and therefore extensive internationally funded programmes have been carried out to determine the pathogen population structure there. Studies from Peru based on virulence, metalayxl sensitivity, allozyme, mt DNA RFLP and AFLP (Perez *et al.*, 2001; Garry *et al.*, 2005) indicate presence of 5 clonal lineages (US-1, EC-1, PE-3, 5, 6) with EC-1 dominating the pathogen population in Andean countries north of Peru. Using similar tools, reports from Ecuador indicate presence of US-1, EC-1, EC-3 and a modified EC-2, which had to be redescribed in view of an extended host range and therefore perhaps another host-adapted clonal lineage (Adler *et al.*, 2004; Erselius *et al.*, 1999b; Oyarzun, 1998). The Mexican populations studied (Goodwin *et al.*, 1992a; Grunwald *et al.*, 2001; Flier *et al.*, 2003) showed that there was little genetic diversity in northwestern parts in contrast to north eastern and central Mexico where almost every single isolate represented a

unique genotype; 81.8% of AFLP loci were polymorphic (Flier *et al.*, 2003), with genetic differentiation between populations from cultivated Potato and wild *Solanum* sps. and first genetic evidence for elevated ploidy levels in *P. infestans* (Goodwin *et al.*, 1992a). Genetic analysis of Mexican isolates for metalyxl insensitive loci showed that it mapped to the same locus as North American and Dutch isolates, as did the British isolates which also mapped to the same linkage group but to a distinct site, *Mex 2*. In Costa Rican potato fields the isolates had no genetic similarity with US-1, US-18 and EC-1 clonal lineages, but had enough diversity to generate 11 RAPD genotypes with the possibility that these shared a common ancestry (Páez *et al.*, 2005).

Analysis of US isolates based on [mating type & *Gpi* (Groves, 2002); mating type, metalyxl insensitivity, *Gpi*, mitochondrial and nuclear (RG57) DNA RFLP (Gavino *et al.*, 2000); mating type metalyxl insensitivity & *Gpi* (Wangsomboondee *et al.*, 2002)] showed that not only had metalyxl resistant lines appeared (Fry, 1997a; b) but also there were implications of sexual reproduction and generation of an aggressive lineage (Gavino *et al.*, 2000). While diversity was high (16 unique multilocus genotypes) in the Columbia basin of Oregon and Washington, in NC, isolates from tomato were genetically more diverse (Wangsomboondee *et al.*, 2002).

Canadian studies based on metalyxl insensitivity, mating type, *Gpi* (Daayf and Platt, 2000) and RAPDs (Peters *et al.*, 2001; Daayf *et al.*, 2001) showed that the population of *P. infestans* changed significantly in mid 1990 with detection of metalyxl insensitive A2 mating types which gave rise to novel (14 unique multilocus) genotypes possibly being generated by asexual reproduction.

In the African subcontinent, the genetic diversity of Ugandan isolates of *P. infestans* analyzed with mitochondrial DNA haplotype and AFLP (Ochwo *et al.*, 2002); and the Kenyan isolates with nuclear RFLP, metalyxl insensitivity, allozyme characteristics (*Gpi* & *Pep*) and aggressiveness showed that these isolates and probably the Rwandan isolates belong to the US-1 clonal lineage, but what was striking was that Sub-Saharan Africa seems to the only area studied to date where two coexisting host-specific population belong to the same clonal lineage (Erselius *et al*, 1999a; Vega-Sanchez *et al.*, 2000).

In the Asian subcontinent, investigating isolates in Korea, India, Taiwan, Indonesia, Thailand, Nepal and China, Nishimura *et al.* (1999) found A2 mating type isolates and Asian-specific allozyme genotypes. Akino *et al.* (2004) showed the existence of a genotype in both China and Japan suggesting the distribution of the SIB-1 lineage in northern Eurasia. Deahl *et al.*, (2002) reported the migration and replacement of Taiwanese population (of US-1) between 1991-2001.Chinese isolates based on mating type, colony growth, ability to grow on oatmeal agar, linear growth rate and amount of sporangia produced showed considerable genetic diversity even though all isolates in the Yunan province was of A1 type (Guo *et al.*, 2002); Nepalese isolates were studied for virulence and race diversity (Ghimire *et al.*, 2001a), mating type (Shrestha *et al.*, 1998; Ghimire *et al.*, 2001b), metalyxl sensitivity (Ghimire *et al.*, 2001b) and nuclear and mitochondrial DNA polymorphisims (Ghimire *et al.*, 2003). Results indicated that even though 11 multilocus genotypes were detected, 3 of them constituted 94% of the total population, indicating limited gene flow, with 30 races having minimal virulence complexity, presence of both A1 & A2 mating types displaying different allozyme genotypes and presence of the old clonal lineage US-1 which was being displaced by new dominant population (NP1) of mtDNA Ia type (Ghimire *et al.*, 2003) in keeping with the global trend.

A recent study (Gotoh *et al.*, 2005) on 401 isolates from eight Asian countries (Korea, India, Taiwan, Indonesia, Thailand, Nepal, China and Japan between 1992-2000, based on mating type, metalyxl resistance, RG57 fingerprint, mt DNA haplotype and 3 allozyme loci (*Gpi*, *Pep*, *Me*) showed the presence of 20 multilocus genotypes of which 14 were new (e.g. NP-1 from Nepal and northern India). Eight multilocus genotypes were found in several regions (e.g. NP-1 and NP1 from Nepal and northern India) providing presumptive evidence that migrations could have occurred between regions in Asia. Interestingly the multilocus NP-1 and NP-2 genotypes have not been reported from other Asian

countries so they may have arisen within Nepal and/ or northeastern India.

In India, diversity and differentiation of *P. infestans* populations have been characterized by RAPD, which revealed that the isolates could be grouped into two geographical location based clusters; hill and plains, with 85% variation in hill isolates (Atheya *et al*, 2005). Characterization for virulence factors and physiological races using 16 differentials showed race spectrum and complexity was much higher in Himachal Pradesh hills than in the Indo-Gangetic plains with virulence factor 1, 3 and 1,7 being the most dominant in Himachal Pradesh hills and Indo-Gangetic plains respectively (Gupta *et al.*, 2005). The A2 mating type first recorded in India in 1991, is displacing the 'old' A1 mating type (Singh and Bhat, 2003; Gupta *et al.*, 2001) due to it's aggressiveness (Singh *et al.*, 2004; Gupta *et al.*, 2003) and increasing insensitiveness to metalayxl (Singh and Shekhawat, 1998) with a resultant increase of the resistant isolates, similar to the phenomenon observed in several parts of the world.

Even though a limited number of markers are currently available, the sheer volume and number of studies made on *P. infestans* (mostly based on cultivated potato) around the globe allows following conclusions to be drawn concerning population structure.

a) Variations detected in most countries is increasing through migration events that have been hypothesized to occur in a two-step (Niederhauser *et al.*, 1954; Fry *et al.*, 1993) or a three-step process (Goodwin *et al.*, 1994a) or perhaps more complexly (Ristanio *et al.*, 2001). The most important event being the secondary result of this migration *i.e.* sexual reproduction of *P. infestans* in Europe as a cause of the second migration (Hohl and Iselin, 1984). Isolates with the A2 mating type and new allozyme genotypes were collected in the Netherlands and eastern Germany as early as 1980 (Daggett *et al.*, 1993; Drenth *et al.*, 1994). These genotypes had spread throughout Europe (Shattock *et al.*, 1990; Spielman *et al*, 1991; Fry *et al.*, 1991; Drenth *et al.*, 1993; Tooley *et al*, 1993; Andrivon *et al.*, 1994a, b; Goodwin *et al.*, 1994b; Sujkowski *et al.*, 1994;) and to the Middle East, Africa (Goodwin *et al.*, 1994b), and South America (Fry *et al.*, 1993) by the early 1990s. Evidence supporting this migration and the associated changes that occurred in *P. infestans* populations worldwide has already been reviewed by many workers (Drenth *et al.*, 1993; Fry *et al.*, 1993; Drenth *et al*, 1994, Shattock and Day, 1996; Fry and Goodwin, 1997b).

b) Clonal lineages dominate most populations, but in some they are accompanied by many rare annual genotypes. The most commonly detected 'old' clonal lineage is the US-1 (Goodwin *et al.*, 1994a), of A1 mating type, with a dilocus allozyme genotype *Gpi* 86/100, *Pep* 92/100 (Spielman *et al.*, 1991) and a characteristic 15 band DNA fingerprint (Drenth *et al.*, 1994; Goodwin *et al.*, 1994a; Goodwin *et al.*, 1995a), mt DNA haplotype A (Goodwin, 1991) and most probably derived from a single Mexican ancestor during the past 134 years. (Goodwin, 1997). US-1 was probably the only genotype of *P. infestans* present in Europe prior to late 1970s and the variations present in the European samples are the result of mutation within US–1 clonal lineage. Although the frequencies varied widely, pathogenicity to all 13 potato and tomato resistance genes tested has been identified within the US-1 clonal lineage. Similar rapid changes in virulence occurred within the US–7 and US–8 clonal lineages in the United States and Canada (Goodwin, 1995b).

c) Populations in Asia are composed of 4 clonal lineages, US-1, the clone that occurs throughout the world (Goodwin *et al.*, 1994b), JP–1 (Koh *et al.*, 1994), Japanese A1–A and Japanese A1–B (Kato, 2000; Akino *et al.*, 2004); the latter two being redesignated as JP–2 and JP–3 respectively by Gotoh *et al.* (2005), with probability of sexual reproduction occurring in Nepal, Thailand and Japan (Gotoh *et al.*, 2005) and with many of the multilocus genotypes probably having arisen there rather than migrating into it. The JP–1 clone in Asia is quite different from the genotypes in other areas and may have originated from a separate introduction. Similarly, the isolates representing single clones in Australia, Bolivia, Brazil, and Costa Rica have unusual genotypes (Goodwin *et al.*, 1992a) that probably were not introduced during any of the four known migrations. However, the genetic diversity in these populations is still a subset of that in Mexico.

d) The spatial heterogeneity is high, even at time scale; this affects the choice of sampling strategies and therefore, the question remains as to how many

samples are needed for an accurate reflection of population structure. It is also not known if there really is any sub-structuring of European or Asian populations or has long range spread by wind and seed (tubers) created a random mosaic?
e) Within many populations, genotypes of both mating types co–exist and oospores are detected in the field, but the frequency of sexual reproduction that generates new variation has not yet been quantified; moreover the cause of the marked spatial-temporal variation in mating type ratios is also unknown.

Considering the diversity of other *Phytophthora* species, the next species whose diversity has been most studied is *P. sojae*. In China the occurrence of the pathogen is found in all the major soybean growing areas and were of 72 virulence types with virulence composition being most diverse and complex in the Yangtze basin (Zhu *et al.*, 2003; Zhu *et al.*, 2004). Northeast isolates could be classified into 3 distinct races (Xu *et al.*, 2003). RAPD analysis showed that there was a high amount of polymorphism (87.2%) and revealed existence of 12 distinct genetic groups but they could not be correlated to virulence or geographical origin of the isolates (Wang, *et al.*, 2003).

Within the US, a survey in Illinois, Indiana, Iowa, Minnesota (Meng *et al.*, 1999) and Ohio (Dorrance *et al.*, 2003) identified the races. RAPD analysis clustered them into 4 distinct groups with diversity being detected among isolates of races 1, 3, 4, 5, 7 and 25 but not among 8 and 13 Rps differentials and with 52% of the locations having at least one isolate with virulence to most of the Rps gene based differentials. Similarly in Canada earlier studies (Anderson and Buzzell, 1992) showed a simpler race structure 1, 3, 4, 5, 6, 7, 8, 9, 13 and 21, with race 3 constituting 24.2%, which was the highest.

A comparative study of Australian and American isolates for virulence and RFLP showed that the Australian population consisted of 5 races (1, 4, 13, 15 and X) with low genotypic diversity of 2.5-14.3% (3 multilocus RFLP genotypes with one occurring in over 95% isolates), in contrast to the high (60%) diversity corresponding to 12 multilocus RFLP genotypes in American population suggesting that the Australian population was established most probably by a single introduction of the pathogen and that the new races evolved from a common genetic background through mutation.

Cocoa being another important cash crop, diversity of *Phytophthora* species on this crop has been studied. *P. megakarya* is the most aggressive followed by *P. citrophthora*, *P. palmivora* and *P. capsici*. Single reports of other *Phytophthora* species include *P. botryose*, *P. heveae*, *P. katsurae* and *P. megasperma*, although they are not considered as major problems for cocoa production (Appiah *et al.*, 2004). Recently molecular analysis using ITS sequences (Appiah *et al.*, 2004) and RAPD (Falerio *et al.*, 2003) was used to assess the intra- and interspecific diversity. The isolates clustered into distinct genus specific groups irrespective of geographical origin. The mating types (Chowdappa and Chandramohanan, 1997; 1998) and the nature of the native total protein profiles (Chowdappa and Chandramohanan, 1995) of the 3 *Phytophthora* species: *P. citropthora*, *P. palmivora* and *P. capsici* causing the disease in India have been studied. Both the A1 and A2 mating types have been found among the *P. palmivora* and *P. capsici* isolates with A2 and A1 predominating in *palmivora* and *capsici* respectively; electrophoretic profiles showed that the isolates of *P. capsici* were highly homogenous forming a single cluster as did *P. palmivora* which grouped separately but *P. citrophthora* isolates resolved into 2 distinct groups. When the same 3 species (which are the major pathogens) were studied in Brazil, using RAPD (Faleiro *et al.*, 2003; Faleiro *et al.*, 2004) and differential sensitivity to fungicides (de-Oliveira and Menge, 1999) they showed different levels of intraspecific variation. A SAHN clustering method showed 2 distinct groups within *P. citropthora* based on host origin and 2 groups within *P. capsici* based on geographical origin.

Polymorphisms were also detected at the level of isoenzymes (Blaha, 1987; Blaha, 1990; Nyasse *et al.*, 1999), RFLPs (Blaha, 1990) and RAPDs (Nyasse *et al.*, 1999) for *P. megakarya*. Within Africa there were 2 highly differentiated genetic groups coinciding with 2 the major biogeographical domains, which may reflect an ancient evolution of *P.*

megakarya in Africa. Genotypic diversity was low in West Africa compared to Central Africa with intermediate marker pattern groups near the border of Nigeria and Cameroon, in addition to the prevalence of A1 over A2.

Morphological characteristics, pathogenicity tests and RAPD showed that the Indonesian isolates of *P. palmivora* causing pod rot of cocoa consisted of a single genetic background different from those pathogenic on coconut (Darmono, 1997). A study using pathogenecity and RAPD on seven population of *P. palmivora* affecting coconut in India showed that majority of the diversity was within the population and there was clear separation based on geographical locations of Karnataka and Kerala population (Sudheesh and Sreekumar, 2006).

Since *P. capsici* infects more than 50 species, diversity of the species has been studied on hosts other than cocoa also. Genetic variation among isolates has been reported from vegetable growing areas of the world [mtDNA RFLP (Hwang *et al.*, 1991); AFLP (Lamour and Hausbeck, 2002); oligonucleotide hybridization to amplified rDNA ITS regions (Lee *et al.*, 1993); AFLP and ISSR (Tian and Babadoost, 2003)]. Differentiation was there with respect to host origin based on RAPD and pathogenicity (Polach and Wenster, 1972; Luz *et al.*, 2003) and geographical origin based on ISSR and AFLP (Tian and Babadoost, 2003) as well as within a single host (Capsicum) based on virulence, metalayxl response and RAPD (Silvar *et al.*, 2006).

P. cinnamomi is another pathogen that additionally causes havoc in forest ecosystems. In Australia both 'morpho-physio-cultural' characteristics like i) growth rate on PDA, V8JA and CMA, ii) colony morphology, iii) sporangial and gametangial morphology, iv) sporangial production, v) mating type (Daniel *et al.*, 2003) and vi) temperature growth relationship (Shepherd and Pratt, 1974), and genetic differentiation based on isoenzymes (Old *et al.*, 1988), RFLPs and RAPDs (Linde *et al.*, 1999) of the isolates were done as with the isolates in South Africa [using RAPDs and RFLPs (Linde *et al.*, 1999), as well as isozyme polymorphisms (Linde *et al.*, 1997)] and in Taiwan [using RAPD and mating type (Chang *et al.*, 1996)]. The Australian isolates were all of the A2 mating type irrespective of geographical origin suggesting variation was derived asexually similar to the situation in S. Africa where sexual reproduction occurs rarely. Gene and genotypic diversity studies showed that isolates from both these countries were almost identical. Analysis of the Taiwan isolates showed that host specified races might occur in *P. cinnamomi*.

Diversity studies have also been carried out on *P. colocasiae* by Zhang *et al.* (1994) in mainland China based on mating type, soluble protein profiling, growth response, morphology of sporangia and by Lebot *et al.* (2003) in Southeast Asia based on RAPD, isoenzyme; *P. clandestina* based on pathogenecity, RAPD profiles (Purwantara *et al.*, 2001; Purwantara *et al.*, 1998); *P. erythroseptica* based on RAPD analysis, mefenoxam sensitivity (Peters *et al.*, 2005); *P. quercina* in European populations based on 260 AFLP markers (Cooke *et al.*, 2005) as well as *P. nicotianae* based on differences in elicitin production (Bonnet *et al.*, 1994; Colas *et al.*, 1998), RAPD (Ning and Xiu-guo, 2001; Zhang *et al.*, 2003) and in India, based on RAPD (Guha Roy, 2007c; Guha Roy *et al.*, 2008), effect of fungicides, biocontrol agents, morphology and mating type of the isolates (Guha Roy *et al.*, 2003; 2007a; 2007b; 2008). Even though *P. nicotianae* is one of the most polyphagous species yet not much study has been undertaken to assess the diversity and it's potential for exhibiting specialization for particular host species.

In recent years, parallel to the resurgence of *Phytophthora* in pathogenic conditions i.e. in fields, and in the news oömycete research has entered an exciting phase due to the technical developments in the last decade. The recent sequencing of the draft genomes of *P. sojae* and *P. ramorum* (Tyler *et al.*, 2006) as well as the genome and mitochondrial haplotypes of *P. infestans* (http://www.broad.mit/annotation/genome/phytophthora_infestans) can be considered as the turning point in our understanding of these organisms. Structural genomic studies under way at the *Phytophthora* Genome Consortium, Syngenta *Phytophthora* Consortium as well as collaborative efforts at Broad Institute, MIT and Harvard University USA have resulted in draft genome sequencing of *P. infestans* (237Mb), *P. sojae*

(95Mb), *P. ramorum* (65Mb) as well as mitochondrial haplotypes of *P. infestans* which will be of tremendous use for the development of genetic markers like single nucleotide polymorphisms (SNPs) for population genetics and strain tracking of the pathogen.

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(Accepted for publication June 30, 2008)