

Rev. Plant Pathol. Vol. 6, 2014
Indian Society of Mycology and Plant Pathology
Scientific Publishers (India), Jodhpur pp. 387-412

THE PLANT DESTROYER GENUS PHYTOPHTHORA IN THE 21ST CENTURY

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KEYWORDS: Aquatic Phytophthoras, Crop/Plantation Phytophthoras,
 Forest Phytophthoras integrated morphological & phylogenetic
 key, multi-host species, putative new species, genome
 sequencing

ABSTRACT

The 21st century has already seen a major paradigm shift in our understanding of the biology, evolution, and genetics of the genus *Phytophthora* as well as the tools and approaches used to develop novel approaches for disease management. The combination of novel tools and approaches provided by the convergence of genome sequencing, computing power and novel genomic/biotechnological tools paints a promising picture of the future of *Phytophthora* disease management. At the same time *Phytophthora* pathogens continue to emerge at an accelerated rate due to increased global travel and trade. This article provides a brief review of the impact, biology and the current genome-enabled era that will characterize progress in the 21st century.

INTRODUCTION

The genus *Phytophthora* has a long history in modern science. The scientific discipline of plant pathology was born in the early 1860s when Anton de Bary recognized *Phytophthora infestans* as the pathogen causing potato late blight responsible for the Irish potato famine in the 1840s (4,5). It also brought about the first formulated use of a fungicide. In addition to this substantial social and historical impact, even considering merely a handful of *Phytophthora* spp. (e.g., *P. sojae*, *P. infestans*) documented to cause significant economic impacts, costs amount to anywhere between 2-7 billions of dollars per crop per year worldwide in combined crop losses and management costs not even considering the less quantifiable but equally large impacts to natural ecosystems severely affected by some species (e.g., *P. cinnamomi*, *P. ramorum*).

TAXONOMY AND BIOLOGY

The genus *Phytophthora* is presently placed in the kingdom Straminipila (7), under the phylum Heterokonta, sub-phylum Pernosporomycotina, class Pernosporomycetes (Oomycetes), subclass Pernosporomycetidae, order Pythiales and family Pythiaceae. The taxonomy of *Phytophthora* has undergone an evolution in the way it has been studied; from the era of six morphospecies groups (119, 95, 109) to the era of phylogenetic clades (23) and ITS fingerprinting based keys (37) and now to a new era of an integrated morphological and phylogenetic key (102).

Validation of new *Phytophthora* taxa in recent years has been supported with phylogenies generated by sequence analysis of the internal transcribed spacer region (ITS) of the ribosomal DNA gene repeat, the translation elongation factor 1- α , β -tubulin and mitochondrial encoded cytochrome oxidase (cox) I, II, and spacer regions (23, 74, 86, 45). The multilocus phylogeny constructed for 82 *Phytophthora* species with seven molecular markers (8) confirmed the presence of the 10 well-supported clades for the genus previously observed (23). Until 2010, 108 recognized *Phytophthora* taxa have been recognized (94), but many more have been described since then, perhaps an indication of the furious pace of discovery of *Phytophthora* species in recent times (Table 1).

Table 1: Newly discovered/re-described species of *Phytophthora* in the last decade

| Year | Name of species | Remarks | Reference |
|------|--|---|-----------|
| 2001 | <i>P. tropicalis</i> Aragaki & Uchida | formerly referred to as <i>P. palmivora</i> MF4 [= <i>P. capsici</i>] | 5 |
| | <i>P. oryzo-bladis</i> Wang and Lu (ex H H Ho) | | 57 |
| | <i>P. pistaceae</i> Mirab. | formerly referred to as <i>P. megasperma</i> s. l. [sensu lato] | 90 |
| | <i>P. ramorum</i> Werres, de Cock & Man In't veld | | 120 |
| 2002 | <i>P. europaea</i> Hansen & Jung | | 71 |
| | <i>P. psychrophila</i> Jung & Hansen | | 71 |
| | <i>P. uliginosa</i> Jung & Hansen | | 71 |
| | <i>P. brassicae</i> de Cock & Man in 't Veld | formerly referred to as <i>P. porri</i> | 81 |
| | <i>P. ipomoeae</i> Flier & Grünwald | | 35 |
| 2003 | <i>P. inundata</i> Brasier, Sanchez- Hernandez & Kirk | formerly referred to as <i>P. sp.</i> O-group | 15 |
| | <i>P. pseudosyringae</i> Jung & Delatour | | 72 |
| | <i>P. nemorosa</i> Hansen & Reeser | | 54 |
| 2004 | <i>P. alni</i> with subsp. <i>alni</i> , <i>multiformis</i> , and <i>uniformis</i> Brasier & Kirk | formerly referred to as alder <i>Phytophthora</i> , a species hybrid [Brasier et al., 1999] | 13 |
| | <i>P. hedraiandra</i> de Cock & Man in't Veld | | 26 |

| | | | |
|------|---|---|-----|
| 2005 | <i>P. kernoviae</i> Brasier, Beales & Kirk | formerly referred to as <i>P. taxon C</i> | 14 |
| 2006 | <i>P. captiosa</i> Dick & Dobbie | | 27 |
| | <i>P. fallax</i> Dick & Dobbie | | 27 |
| | <i>P. foliorum</i> Donahoo & Lamour | | 29 |
| | <i>P. polonica</i> Belbahri, Melgarejo & Leford | | 7 |
| 2007 | <i>P. alticola</i> Maseko, Coutinho & M.J. Wingf. | | 88 |
| | <i>P. austrocedrae</i> Gresl. & Hansen | | 42 |
| | <i>P. frigida</i> Maseko, Coutinho & MJ Wingf | | 88 |
| | <i>P. siskiyouensis</i> Reeser & EM Hansen | | 101 |
| | <i>P. rubi</i> (Wilcox and Duncan) Man in 't Veld, comb. nov. | formerly referred to as <i>P. fragariae</i> var. <i>rubi</i> | 81 |
| 2008 | <i>P. bisheria</i> Abad ZG, Abad JA & Louws | | 2 |
| | <i>P. asparagi</i> | formerly referred to as <i>P. megasperma</i> s. l., <i>P. taxon asparagi</i> | 105 |
| | <i>P. gallica</i> T Jung & J Nechwatal | formerly referred to as <i>P. taxon G</i> | 68 |
| | <i>P. irrigata</i> C Hong & M Gallegly | formerly referred to as <i>P. drechsleri</i> s. l. [Dre I subgroup] | 58 |
| | <i>P. parsiana</i> Mostowfizadeh, Cooke & Banihashemi | | 91 |

| | | | |
|------|--|--|-----|
| | <i>P. pinifolia</i> AJ. Durán, Gryzenh. & MJ Wingf | formerly referred to as <i>P. cryptogea</i> or <i>P. drechsleri</i> | 31 |
| | <i>P. quercetorum</i> Balci & Balci | | 6 |
| 2009 | <i>P. menzei</i> G.T. Browne, M.E. Gallegly & C.X. Hong | formerly referred to as <i>P. citricola</i> s. l. [avocado subgroup] | 59 |
| | <i>P. multivora</i> PM Scott & T Jung | formerly referred to as <i>P. citricola</i> s. l. / ' <i>P. citricola</i> complex' | 108 |
| | <i>P. plurivora</i> T. Jung and T.I. Burgess | formerly referred to as <i>P. citricola</i> s. l. / ' <i>P. citricola</i> complex' or <i>P. inflata</i> | 67 |
| | <i>P. rosacearum</i> EM Hansen & Wilcox | formerly referred to as <i>P. megasperma</i> s. l. [AC subgroup] | 55 |
| | <i>P. sansomeana</i> EM Hansen & Reeser | formerly referred to as <i>P. megasperma</i> s. l. [DF subgroup] | 55 |
| | <i>Phytophthora X pelgrandis</i> W.F. Gerlach, Nirenberg & Graffenh | | 96 |
| 2010 | <i>P. andina</i> Adler & Flier | formerly referred to as <i>P. infestans</i> s. l., | 97 |
| | <i>P. chrysanthemi</i> Naher M, Watanabe, H., Chikuo, Y., & Kageyama | | 93 |
| | <i>P. hydropathica</i> Hong, C. and Gallegly, M. | Previously termed taxa Dre II. Closest relatives, <i>P. parsiana</i> and <i>P. irrigata</i> (Dre I). High temperature tolerant and isolated from irrigation water | 61 |
| | <i>P. morindae</i> Abad ZG & S Nelson | In ITS clade 10 and most closely related to <i>P. kernoviae</i> but differ in having umbellate sporangiophores. Host: Indian mulberry, <i>Morinda citrifolia</i> L. var. <i>citrifolia</i> | 94 |

| | | | |
|------|--|--|-----|
| 2011 | <i>P. glovera</i> Z.G. Abad & H.D. Shew | In ITS clade 2 and most closely related to <i>P. capsici</i> but differs in being homothallic and produces both paragynous and amphigynous antheridia. Host :Tobacco | 3 |
| | <i>P. gibbosa</i> T. Jung, M.J.C. Stukely & T.I. Burgess, sp. nov. | In ITS clade 6 and associated with dying vegetation in swampy or water logged areas | 69 |
| | <i>P. gregata</i> T. Jung, M.J.C. Stukely & T.I. Burgess, sp. nov. | | 69 |
| | <i>P. litoralis</i> T. Jung, M.J.C. Stukely & T.I. Burgess, sp. nov. | In clade 6 and present in water ways | 69 |
| | <i>P. thermophila</i> T. Jung, M.J.C. Stukely & T.I. Burgess, sp. nov. | In clade 6 and present in water ways; previously been misidentified as <i>P. drechsleri</i> and is referred to as <i>P. sp. 3</i> (Burgess et al. 2009) | 69 |
| | <i>P. himalsilva</i> Vettraino, Brasier & Vannini, sp. nov. | In ITS Clade 2 and forms part of a species cluster defined as Clade 2c by Blair et al. (2008) | 116 |
| | <i>P. pini</i> Leonian, 1925 Emend. Gallegly, Hong, Richardson & Kong = <i>Phytophthora citricola</i> I Gallegly & Hong 2008 | Formerly known as <i>Phytophthora citricola</i> Cil I type (Kong et al. 2003, Gallegly and Hong 2008) | 60 |
| | <i>P. obscura</i> Grünwald & Werres, sp. Nov. | Defines a novel subclade 8d with close relatives <i>P. Syringae</i> and <i>P. Austrocedrae</i> | 43 |

Although there have been considerable advances in the taxonomy of these organisms, the identification to species level using molecular characters remains a major challenge for plant pathologists. Several species "complexes" can be observed in

phylogenetic trees showing the presence of potential cryptic species. Presently, powerful molecular techniques combined with morphological characterisation and a renewed interest in probing of the environments have led to discovery of new species, novel variants within species, hybrids and provided a better resolution of species “complexes” with differentiation of the species therein (46).

There are numerous putative new species, which are in progress for official description in different laboratories around the world. These include *Phytophthora* (*P.*) taxa, such as *P. taxon* Pgchlamydo, *P. taxon* walnut, *P. taxon* oaksoil, *P. taxon* forestsoil, *P. taxon* riversoil, *P. taxon* salixsoil, *P. taxon* raspberry, *P. taxon* Banksia, *P. taxon* meadii-like, *P. taxon* chicory, *P. taxon* Acer, *P. taxon* Agathis, *P. taxon* orphan. Most of these originate from natural ecosystems and are shown to belong to the ITS clade 6 (7, 10, 23). Others are *P. taxon* paludosa (69), *P. sp.* personii (8) *P. taxon* rosacearum-like, *P. taxon* kwongan, *P. taxon* hungarica and *P. taxon* sulawesiensis. Many of these belong to clades 7 or 11 and are so far found only in Australian natural ecosystems where they are associated with plant mortalities (19). The discoveries of natural hybrids have added another dimension (9, 13, 82, 84, 38). And this is not the end; the following provisionally named species are awaiting their validation: *P. cuyabensis*, *P. hungarica*, *P. lagoariana*, *P. niederhauserii*, *P. parvasperma*, *P. sulawesiensis* and *P. sylvatica* (= *P. taxon* forestsoil?). Some, like *P. niederhauserii*, *P. asparagi*, *Phytophthora gemini* although not yet described formally, have been proposed as new species (4, 105, 82).

With the advent of molecular techniques, the most rapid resolution and differentiation of species has been in the ITS clades 2, 3, 6 & 7 (23). This, in some cases, has necessitated division into sub-clades; viz. clade 6, which previously consisted of only three species: *P. gonapodyides*, *P. humicola* and *P. megasperma* (33) has now radiated to the extent that it can be subdivided into 3 sub clades with 11 described species, many *P. taxons* and undescribed species (69). With description of more species in ITS clade 2, it has now been suggested that Clade 2c (8) has evolved within Asia (116).

Considering that there are 200- 600 extant *Phytophthora* species (10), a large number of species therefore remain to be discovered. Once more species are discovered and described,

clearer and well resolved species boundaries will emerge, resulting in revised phylogeny reconstructions. For example, it has become clear that *P. citricola* formerly recognized as a single taxon in phylogenetic reconstructions (23, 8) is now split into a group of species including *P. multivora* and *P. plurivora* (67). As more sequence data become available and new species are described, a clearer picture of species boundaries will emerge.

Host ranges of *Phytophthora* species can vary from one extreme of being very diverse (*P. ramorum*, *P. cinnamomi*, *P. nicotianae*) to that of a single host (*P. sojae*). Host ranges of new invasive forest or other *Phytophthora* species are being determined but the range continues to expand with passage of time (48, 107). Molecular validation and renaming of species are now often increasingly changing host boundaries for each species (e.g. *P. palmivora* MF4 [= *P. capsici*] - *P. tropicalis*). A comparative proteomics study between *P. ramorum* (broad host range) and *P. sojae* (single host range) identified some candidate proteins that might be factors involved in determination of host range (105), but more such comparisons are needed with other broad host range species whose genomes have been sequenced like *P. capsici* and *P. nicotianae* for validation and refinement. As host-pathogen (*A. thaliana*-*P. nicotianae*) interaction models for broad host range are also available (118), the focus perhaps needs to shift to multi-host species and finding the determinants for host specificity which would provide insights for control of these species which cause the most economic impact worldwide but have been difficult to control. Also, as proposed (89), species diverge by geographic isolation (allopatric) or, in the case of pathogens, by a switch in host (sympatric e.g. *P. infestans* - *Phytophthora mirabilis* - *Phytophthora ipomoeae*) and hence it is highly unlikely that two closely related species are able to diverge if they share a common host in the same geographical area. The study of host ranges will therefore become increasingly important in the future to answer questions of potential hosts of invasive pathogens and their speciation and emergence.

IMPACT

Phytophthora pathogens have a large impact on native ecosystems, forests and agricultural crops. The past decade has seen the discovery of a large number of *Phytophthoras* especially

from aquatic and forest ecosystems and a wealth of information is now available on some of the Phytophthoras attacking crops and plantations. These advances and their possibilities will only be discussed here as exhaustive reviews are already available on the subject (75, 51). Here, we selected a few major examples from three distinct habitats: Crop/plantations, forests, and aquatic environments.

Crop/Plantation Phytophthoras

For the most studied of all Phytophthoras, namely *Phytophthora infestans*, the population structure has changed dramatically in the 21st century due to migrations and establishment of sexual populations in select areas. In fact, at very few locations is the population structure similar to what it was in the 20th century. The populations in Mexico (which is thought to be the source of recent migrations) are sexual and this region represents the centre of origin of this pathogen (49, 35, 45). Populations in Asia, North America, South America and north of Mexico have changed and remain mostly clonal while population in parts of Europe have become sexual (36). Recent analysis of simple sequence repeats has revealed diversity within US clonal lineages (for e.g. US 22) (Fry, personal communication) and some new types have also been identified (92). Eucablight and now Euroblight are two websites of the concerted EU networks that rely on extensive multiplexed SSR analyses (78) for surveillance. These efforts have established that while 'blue 13' is a new virulent 'SSR genotype' found in most places in Europe, in France there has been a spatiotemporal change in population structures and a change in allele frequencies in the UK, suggesting a suspected gradual change in populations. A new set of multiplexed SSR primers (79) have revealed that some of the 'SSR genotypes' obtained by using the Eucablight primers could further be subdivided into more genotypes; the converse was also true (20). Targeting of different loci may bring about finer resolution of some of the SSR genotypes; however, if the resultant "groupings/clusters/SSR genotypes" is to be of practical field value towards control of the disease, then each of these SSR genotypes have to be correlated with phenotypic characters like mating type, fungicide sensitivity, growth temperature etc. Implementation of effective control strategies requires knowledge about the genetic

structure of population of plant pathogens (122), as control strategies must target a population instead of an individual if they are to be effective. Defining the genetic structure of a population is a logical first step in studies of fungal population genetics because the genetic structure of a population reflects its evolutionary history and its potential to evolve: aspects important for formulating disease management strategies. Genetic diversity analyses of populations at these locations have therefore become a priority.

P. capsici in many parts of the world are the most important factors limiting vegetable production (52, 75, 123). An excellent review on the population structures and host ranges in both the Americas and Korea on *P. capsici* is available (75). Interestingly the populations of *P. capsici* are very diverse in the US and clonal in neighbouring countries in contrast to the clonal nature of *P. infestans* found in the USA. *P. capsici* additionally affects plantation crops like bell pepper, betelvine and cocoa in countries like India and Vietnam. Populations in India have been found to have intraspecies variation depending on host and techniques used (21) while population diversity is lower in Vietnam (112). Cocoa isolates were however of a single clonal lineage in both countries.

P. nicotianae affects over 255 plant genera in 90 families (22) and is relatively neglected (by scientists and policy makers) considering that this species is one of the most common pathogens on ornamental plants, the cultivation and trade of which has been recognized as a principal pathway for the introduction and spread of invasive plant pathogens (cited in 80). Also it is a major pathogen of different vegetables in some tropical economies. The neglect is potentially influenced by having an extremely broad host range that makes estimation of economic impact difficult. The intraspecific variation of *P. nicotianae* was studied variously by RAPD [tobacco isolates, (124); vegetable and fruit isolates, (52)]; AFLP [floricultural hosts, (77) tobacco, (110)] and variable mitochondrial intergenic regions [various hosts, (80)]. The results were similar showing that intraspecific variability exists and in some cases were related to hosts. The future course of action for both *P. capsici* and *P. nicotianae* would be to find out the extent of the variability with special reference to host specificity.

P. sojae with a single host is considered to be a low risk pathogen because of limited outcrossing and low mutation and has been extensively reviewed (118). However, it is evident that pathotype structures, in clonal populations, are changing (30).

Forest *Phytophthoras*

There are many prominent forest *Phytophthora* species. Perhaps most notable is the sudden oak death epidemic caused by the pathogen *P. ramorum* (48, 104). This pathogen emerged simultaneously on rhododendrons in gardens, woodlands and nurseries in Germany and forests and nurseries in the USA. Sudden oak death is only found in the USA where coast live oak and tanoak forests are severely impacted. However, a recent significant epidemic on Japanese larch has been documented in the UK that is of global concern (12). In both Europe and North America the pathogen exhibits a very broad host range that makes control exceedingly difficult. *P. ramorum* is obviously an exotic pathogen that has been introduced into the US and Europe from elsewhere. Currently, three clonal lineages are being recognized that have been named after the continent (NA = North America; EU = Europe) on which they were first found (47). EU1 only affects Europe, while all three lineages are found in the US (40,39). It has also become evident that the EU1 clonal lineage was moved from Europe to the Pacific Northwest, either British Columbia, Canada or Washington, US, most likely via movement of ornamental plants such as *Rhododendron* spp. (39). The origin of this pathogen is not well established, but recent coalescent analysis determined that the three lineages are either reproductively isolated or geographically isolated even though both mating types exist and have diverged before the rise of modern agriculture (40). Several studies have monitored and described establishment, migration and clonal divergence within each of the continents on which *P. ramorum* is observed (40, 39, 115, 87, 99, 98). Despite the occasional presence of both mating types in nursery environments of the Western US, sexual reproduction has to date not been found (38).

Another prominent forest *Phytophthora* is *P. lateralis* affecting Port Orford Cedar in the Pacific North Western US (56). Like *P. ramorum* this pathogen is introduced to the US and has become a new pathogen on a new host. Unlike *P. ramorum*, *P.*

lateralis has only one known host. Recent work indicated that this pathogen originated in Asia (11). It is thought that *P. ramorum* might also have originated from Asia, but this remains to be established.

There exist numerous other forest *Phytophthora* species of which notable examples include *P. kernoviae* (14) and *P. alni* (13).

Aquatic *Phytophthoras*

Though *Phytophthora* species are commonly referred to as water moulds, little is known about their aquatic ecology and the species present in these habitats are poorly characterized relative to those present on crops. More than 25 species of *Phytophthora*, (including *P. ramorum*, the sudden oak death pathogen), have been isolated from irrigation reservoirs and natural waterways in riparian ecosystems and as well as from swampy or water-logged areas (17, 111, 121, 63,101, 58, 61, 69). A number of previously unknown taxa also have been documented in aquatic environments (15, 58, 68, 69). Systematic sampling efforts have been undertaken for early detection of these pathogens and because of the renewed interest in the assemblage of *Phytophthora* species already resident in streams in natural ecosystems: in western North America (101), south Eastern America (64, 65), South China (123) and Australia (69). However, such efforts are lacking in the Indian subcontinent.

Most of the species found in aquatic environments belong to clade 6 and show a strong association with both forest and riparian ecosystems and, with the exceptions of *P. taxon asparagi*, *P. gonapodyides*, *P. megasperma* and *P. rosacearum*, which have limited association with agriculture and horticulture. However all ITS Clade 6 members are not aquatic, such as *P. pinifolia*, *P. inundata*, *P. taxon PgChlamydo* and *P. gonapodyides* which can be opportunistic and sometimes aggressive tree pathogens (18, 31, 68, 70). The function of most of these taxa within the ecosystems is unclear. It has been hypothesized (15, 17) that a saprotrophic lifestyle and sexual degeneration for taxa in this clade may be connected to their aquatic habitat. Furthermore, due to the almost complete absence of heterothallism within Clade 6 and a lack of records of Clade 6 taxa from the tropics, it has been hypothesised (69) that a tropical origin seems unlikely. Whatever their origin

might be, the fact that recycling of water for irrigation is becoming increasingly important, baiting or filtering irrigation water for pathogenic *Phytophthora* species will increasingly become a useful monitoring tool in agricultural systems, including nurseries (63).

GENOME-ENABLED BIOLOGY

Three *Phytophthora* genomes have been sequenced to date and these include *P. sojae*, *P. ramorum* and *P. infestans* (114, 53). Several other genomes are considered, being or have been sequenced including *P. parasitica*, *P. cinnamomi* and *P. capsici* among others. Comparative genomics of these genomes has revealed a remarkable diversity of effectors that include avirulence genes now referred to as RxLR genes for a conserved amino acid motif characterizing this unique class of small secreted proteins.

Availability of whole genome sequences provides novel tools and approaches for research and translational applications of research. For example, discovery of mating type gene, metalaxyl resistance genes, and other functional and or adaptive traits is within grasp. With a novel class of functional genetic markers plant pathologists will be able to characterize *Phytophthora* populations more accurately and more rapidly, while breeders will be able to pyramid resistance genes more appropriately while using the discovered effect or repertoire for effect or-mediated R-gene discovery (43, 117).

CONCLUSIONS

Phytophthora biology currently is an area of work for plant pathologists undergoing rapid discovery of new species and brimming with the hope of novel, genome-enabled translational discoveries. The *Phytophthora* community is hoping to sequence the genome of each known *Phytophthora* species in a concentrated effort, which will provide a useful, novel platform for development of targeted disease management strategies and result in novel insights about the evolution and patterns of emergence of this important plant pathogen genus.

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