REVIEW

***Phytophthora* Genomics: The Plant Destroyers' Genome Decoded**

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The year 2004 was an exciting one for the *Phytophthora* research community. The United States Department of Energy Joint Genome Institute (JGI) completed the draft genome sequence of two *Phytophthora* species, *Phytophthora sojae* and *Phytophthora ramorum*. In August of that year over 50 people gathered at JGI in Walnut Creek, California, for an annotation jamboree and searched for the secrets and surprises that the two genomes have in petto. This culminated in a paper in *Science* in September of this year describing the highlights of the sequencing project and emphasizing the power of having the genome sequences of two closely related organisms. This MPMI Focus issue on *Phytophthora* genomics contains a number of more specialized manuscripts centered on gene annotation and genome organization, and complemented with manuscripts that rely on genomics resources.

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Convergent evolution of plant destroyers.

Phytophthora literally means plant destroyer, a name coined by Anton de Bary in 1861 when he proved that a microorganism, designated as a fungus, was the causal agent of a plant disease known as late blight of potato and was responsible for the Irish potato famine (Large 1940). The genus *Phytophthora* belongs to the oomycetes, a diverse group that includes both saprophytes and pathogens of plants, insects, fish, vertebrates, and microbes. Among the plant pathogenic oomycetes are more than 65 *Phytophthora* species, a hundred or more *Pythium* species, and a variety of obligate biotrophs, including downy mildews and white rusts (Agrios 2005; Erwin and Ribeiro 1996). They cause devastating diseases on numerous crops, ornamentals, and native plants and have an enormous impact on agriculture. Oomycetes are classified as Stramenopiles or Heterokonts which, together with the Alveolates, form the Chromalveolates, one of the five supergroups in the tree of eukaryotes (Fig. 1) (Keeling et al. 2005). The last common ancestor of the Stramenopiles and perhaps all of the Chromalveolates was most likely photosynthetic with a plastid captured from red algae by secondary endosymbiosis. This plastid was

subsequently lost by some lineages, including the heterotrophic oomycetes, but was maintained by other lineages, such as the delicate unicellular diatoms and the brown algae, with the magnificent giant kelp as a prominent example. The photosynthetic ancestry of the various Stramenopile lineages is supported by the presence of numerous genes of putative phototrophic origin in *Phytophthora* spp., with over one third of these (295 out of 855) shared by the diatom *Thalassiosira pseudonana* (Tyler et al. 2006).

Another major group of plant destroyers comprises the fungi, classified in the supergroup Unikonts (Keeling et al. 2005). With respect to growth morphology (mycelium) and propagation (via spores), oomycetes and fungi are look-alikes, but their physiology, biochemistry, and genetics differ. Nevertheless, their weaponry to attack plants is quite similar. They employ similar infection structures, such as appressoria and haustoria, and share an extensive repertoire of cell wall-degrading enzymes to weaken host tissue (Judelson and Blanco 2005; Latijnhouwers et al. 2003). Fungal and oomycete plant pathogens occupy similar ecological niches. Yet the distinct evolutionary history of the two groups implies that their pathogenic behavior evolved independently and that convergent evolution has shaped the genomes of these two major groups of plant pathogens.

Genome projects of plant destroyers.

Only in recent years have genomes of eukaryotic plant pathogens been sequenced. The first one was *Magnaporthe oryzae*, the rice blast fungus (Dean et al. 2005), and to date, a handful of draft genome sequences of fungal plant pathogens are available (Xu et al. 2006). Overall, the genome sizes of fungi do not exceed 40 Mb and they are mostly haploid. In contrast, the genomes of oomycetes studied so far are all larger than 45 Mb and often double that size or more and they are diploid (Judelson and Blanco 2005; Kamoun 2003). It is, therefore, not surprising that it took some time before oomycete genome projects got off the ground. Besides limitations faced by funding, further development of assembly algorithms and software needed to occur in order to handle whole shotgun sequence reads from relatively large diploid genomes. Advances in software and sequencing technologies have resulted in a decrease in costs and a sharp increase in the number of ongoing eukaryotic genome sequencing projects, and fortunately, oomycete sequencing projects are also on the rise (Table 1).

One incentive for funding a *Phytophthora* genome sequencing project was the emergence of a mysterious disease threatening California oak trees. *Phytophthora ramorum*, the causal agent of Sudden oak death, was described as a new

Corresponding authors: Francine Govers; E-mail: francine.govers@wur.nl and Mark Gijzen; E-mail: gijzenm@agr.gc.ca. MPMI Senior Editors Oomycete-Plant Interactions, 2000–2006 and from 2007, respectively.

species in 2001 (Werres et al. 2001), and only four years later, a draft sequence of its genome was available. Emotion and scientific rationale clashed. The Californians cried because their magnificent oak trees were dying and they wanted immediate action to solve the problem. But the scientists raised doubts about the value of sequencing the genome of a relatively unknown species that had no history of research and that few people studied. The compromise was to include a second species, *Phytophthora sojae* that, next to 'the Irish potato famine fungus' *Phytophthora infestans*, has the status of being a model for molecular genetic research on oomycetes. *P. sojae* was first described in the 1950s as the causal agent of root and stem rot on soybean (Hildebrand 1959; Kaufmann and Gerdemann 1958). Thus *P. infestans* and *P. sojae* each attack major food and feed crops and are devastating pathogens worldwide. Because of their economic impact, the two species have been studied in detail for many years and the necessary tools, such as DNA transformation, gene-silencing, and genetic linkage maps, are available (Birch and Whisson 2001; Judelson and Blanco 2005; Kamoun 2003; Tyler 2001). Also, the first oomycete expressed sequence tag (EST) projects involved these two species (Kamoun et al. 1999; Qutob et al. 2000) and in recent years many more *P. infestans* and *P. sojae* EST were generated (Randall et al. 2005; Torto-Alalibo et al. submitted).

Comparative genomics: The surplus value of two genomes.

The proposal to sequence two genomes in parallel was a pleasing compromise that appealed to both the social and the scientific interests focused on *Phytophthora* diseases. Although analysis of a single genome provides tremendous biological insights for any given organism, comparative analysis of multiple genomes can provide substantially more information on the physiology and evolution of genomes and increases our ability to identify and assign putative functions to predicted coding regions. Of the 19,027 predicted genes in *P. sojae* (called gene

models) and 15,743 gene models in *P. ramorum*, 9,768 seem to have the same function. The orthologs are arranged in very similar orders along the chromosomes, and this helped in assembling the sequence and placing the scaffolds in the right order and orientation. For *P. sojae*, the sequence assembly was also facilitated by the availability of a physical map. In this issue, Zhang and associates (2006) describe the physical mapping of 8,681 bacterial artificial chromosomes (BAC), resulting in 257 contigs. Merging these BAC contigs with 207 sequence scaffolds led to a consensus physical map consisting of 79 superscaffolds.

Comparative genomics of species within a single genus can reveal the dissimilarities that may account for the biological characteristics of a given species. In *Phytophthora* spp., host specificity is a typical characteristic that differs between species. Interestingly, comparison of regions of conserved synteny in *P. sojae* and *P. ramorum* revealed that the conserved synteny is often interrupted at places harboring genes encoding proteins with putative functions in the interaction with host plants. One example, described by Jiang and associates (2006a, this issue), concerns a region containing the race-specific avirulence gene *Avr1b-1*, which encodes a protein belonging to the RxLR-dEER super family. *P. ramorum* lacks a homolog of *Avr1b-1* and homologs of many other members of the RxLR-dEER super family. On the other hand, *P. ramorum* has a set of genes encoding RxLR-dEER proteins that are absent in *P. sojae*. Overall *P. sojae* has 1,755 genes and *P. ramorum* 624 that have no homolog in the other genome (Tyler et al. 2006), and a subset of these belongs to the RxLR-dEER super family.

Comparative genomics also revealed that the larger size of the *P. sojae* genome (95 Mb compared to 65 Mb in *P. ramorum*) is not only due to slightly larger numbers of predicted genes or larger gene families but also to larger intergenic regions and large segments of genome sequences absent in *P. ramorum*. Both genomes contain numerous open reading frames (ORFs) with similarities to retrotransposons and other transposable-like

Fig. 1. A schematic phylogeny of eukaryotes. This hypothetical tree was drawn according to recent reviews by Baldauf (2003) and Keeling and associates (2005). The five proposed eukaryotic supergroups are shaded and labeled in bold font. For simplicity, other labels correspond to selected examples; major sub-branches are shown in italics, and representative groups of organisms are provided at the branch termini. Plantae, Rhizaria, Chromalveolates, and Excavates represent the bikont lineages.

elements (Tyler et al. 2006), and the retrotransposons show different expansion patterns in different lineages (Jiang and Govers 2006). In *P. infestans*, which has an extraordinarily large genome of around 240 Mb, intergenic regions are often larger than in *P. sojae* (Jiang et al. 2006b), but also, the different types of transposons found in this species are overwhelming (Ah Fong and Judelson 2004; Jiang et al. 2005; Judelson 2002). The variation in genome sizes within the *Phytophthora* genus may be due in part to differences in transposon activity.

Tripathy and Tyler (2006, this issue) analyzed the transfer (t)RNA genes in the two *Phytophthora* genomes. In line with genome size and numbers of gene models, *P. sojae* has more tRNA genes than *P. ramorum* (208 versus 140). They code for 45 different tRNA anticodons. For 14 tRNA anticodons, tRNA genes are absent in both genomes. Nevertheless, analysis of codon usage showed that these codons are present in *Phytophthora* ORFs, and probably, the missing anticodon types of tRNAs are compensated by wobbling of other tRNA anticodons. The absence of specific tRNA genes seems to be correlated to the codon usage bias in *Phytophthora* genomes. Predicted ORFs in genus *Phytophthora* have a relatively high percent G+C, which can be 8 to 10 % higher than the average percent G+C in the genome. This increase is mainly due to a much higher percentage of G+C at the third codon position (GC3). Qutob and associates (2000) used the high GC feature to discriminate *P. sojae* ESTs from soybean ESTs in a cDNA library from infected soybean hypocotyls, and Jiang and Govers (2006) showed that GC3 frame plots can be exploited as a tool to predict the position of genes on large sequence scaffolds of *Phytophthora* spp. Biases in codon usage can be due to selection pressure exerted by translation processes and only affecting coding regions or to a more global mutation bias acting on all sequences, coding and noncoding. The absence of specific tRNA genes and the abundance of the various tRNA species may have driven adjustments of codon usage in *Phytophthora* spp., but also whole-genome mutation bias seems to play a role. *P. sojae* and *P. ramorum* show a different degree of codon bias, and the average percent G+C in noncoding regions is significantly higher in *P. sojae* (Jiang and Govers 2006).

Another remarkable difference between the two sequenced species is the percentage of nuclear mitochondrial DNA or NUMTs. NUMTs, which are nuclear DNA fragments that are homologous to mitochondrial DNA, are common in eukaryotes. In different organisms, the number and sizes of NUMTs and the degrees of similarity to their mitochondrial counterparts vary, and even among species of related genera, like human and mouse or *Arabidopsis* and rice, substantial differences are found. Krampis and associates (2006, this issue) were the first to analyze NUMTs in two species belonging to the same genus.

In *P. sojae*, the NUMT content is sevenfold higher than in *P. ramorum*. Since the *Phytophthora* NUMTs have a nearly perfect sequence identity with their respective mtDNA, transfer from the mitochondrial genome to the nuclear genome likely occurred after divergence of the two species. In *P. sojae*, however, more frequent alterations in the NUMTs were observed, probably as a result of insertions, duplications, inversions, and translocations. Whether this implies that, overall, genome rearrangements occur more frequently in *P. sojae* than in *P. ramorum* remains to be answered. Nevertheless, analyzing NUMT content and sequence diversity likely provides insight into active mechanisms that govern genome evolution in individual species.

All together, the comparison between *P. sojae* and *P. ramorum* revealed that *P. sojae* has a larger genome size, more genes, larger intergenic regions, larger gene families, more diverse NUMTs, a more biased codon usage, and higher G+C content. Apparently, each genome evolves at its own pace. *P. ramorum* seems to be able to keep its genome more streamlined without losing strength as a pathogen. It will be interesting to extend these analyses to other *Phytophthora* species and to search for correlations with, for example, host specificity or ability to avoid host resistance or adapt to new environments.

What makes the genus *Phytophthora* unique?

Many mycology and plant pathology textbooks list features that distinguish oomycetes from true fungi. The biflagellated zoospore is one such feature but also sterol auxotrophy and the cellulose backbone of cell walls rank high on the list. The gene annotation confirmed that *Phytophthora* spp. lack genes that are common in fungi, such as the ones encoding particular cytochrome P450 enzymes necessary for sterol biosynthesis or the polyketide synthases required for biosynthesis of secondary metabolites (Tyler et al. 2006). It also revealed that *Phytophthora* spp. have a much larger repertoire of secreted proteins than the autotrophic diatom *T. pseudonana* and that several classes of secreted hydrolases are shared by plant pathogenic fungi and oomycetes. Only 21% of the *Phytophthora* gene models have similarity to known proteins, whereas another 57% contain matches to known protein motifs. This implies that 23% are not found in species other than *Phytophthora* spp., many of which (1,563) are orthologs present in both species. Novel genes are intriguing. Are they keys to potential drug targets for oomycetes?

One paper in this issue (Meijer and Govers 2006) is devoted to the annotation of genes involved in phospholipid signaling and focuses on one of the many biochemical pathways ubiquitous in eukaryotes. The 58 gene models that are described are all highly conserved in the two *Phytophthora* species but very few resemble proteins known in other eukaryotes. For those few, the enzymatic function can be predicted, but for the ma-

Table 1. Current status of oomycete genome sequencing projects (September 2006)

Species	Genome size	Coverage	No. genes ^a	Sequencing center ^b	URL
<i>Phytophthora sojae</i>	95 Mb	9x	19,027	JGI	genome.jgi-psf.org/sojae1/sojae1.home.html phytophthora.vbi.vt.edu ^c
<i>Phytophthora ramorum</i>	65 Mb	7.7x	15,743	JGI	genome.jgi-psf.org/ramorum1/ramorum1.home.html phytophthora.vbi.vt.edu
<i>Phytophthora infestans</i>	240 Mb	8x	na	BI	www.broad.mit.edu/annotation/genome/phytophthora_infestans
<i>Phytophthora capsici</i>	65 Mb	2x/20x ^d	na	JGI	www.jgi.doe.gov/ and www.ncgr.org ^e
<i>Hyaloperonospora parasitica</i>	75 Mb	8x	na	WUGSC	accessible via phytophthora.vbi.vt.edu

^a Number of annotated full-length genes.

^b JGI = Joint Genome Institute; BI = Broad Institute; WUGSC = Washington University, Genome Sequencing Center.

^c Community annotation database hosted by the Virginia Bioinformatics Institute (VBI) (Tripathy et al. 2006).

^d 2x coverage based on Sanger sequencing and 20x coverage based on 454 sequencing.

^e Expected to be posted in early 2007.

jority, the combinations of structural and regulatory domains are merely an indication that they play a role in this particular pathway. They may as well have other substrates of which we are completely unaware. Remarkably, in several of the gene models phosphatidylinositol phosphate kinase domains or catalytic phospholipase D domains occur in association with transmembrane domains. There is, for example, one family with 12 members that have a characteristic N-terminal seven-transmembrane G-protein coupled receptor (GPCR) signature and a C-terminal phosphatidylinositol phosphate kinase (PIPK) domain. This is a completely novel protein. So far, only one homolog has been found outside the genus *Phytophthora*, and that is RpkA in *Dictyostelium discoideum*, a GPCR-PIPK crucial for cell-density sensing (Bakthavatsalam et al. 2006). These findings nourish the thought that the genus *Phytophthora* has developed a sensing system that bypasses heterotrimeric G proteins.

The unusual features and domain compositions that Meijer and Govers (2006) observed in the majority of the 58 gene models is not unprecedented. A recent study on myosin domain evolution showed that the genus *Phytophthora* has the highest number of myosin types found in any sequenced eukaryote, 13 of the 37 different types identified. Strikingly, nine out of these 13 were not found in any other eukaryote. The human species (*Homo sapiens*) has 12, two of which overlap with *Phytophthora* types, whereas the diatom *T. pseudonana* has only three types and *Plasmodium falciparum* two (Richards and Cavalier-Smith 2005).

The pathway that Meijer and Govers (2006) analyzed starts with phosphatidylinositol and results in the synthesis of phosphatidic acid. One of the four steps normally requires a phospholipase C (PLC), an enzyme with conserved features present in all eukaryotes sequenced so far. Surprisingly, *Phytophthora* spp. have no such PLC gene. How *Phytophthora* spp. cope without a PLC gene is still unresolved and is just one of many questions that will arise when the genomes are mined for enzymes involved in other metabolic and signaling pathways.

Pathogenicity relies on protein targeting motifs.

A major breakthrough that occurred in the midst of the annotation jamboree was the discovery of the oomycete RxLR-dEER motif. At the time, the first genes encoding oomycete Avr proteins were just becoming known. There was Avr1b-1 from *P. sojae* (Shan et al. 2004), ATR13 and ATR1^{NdWs} from the downy mildew *Hyaloperonospora parasitica* (Allen et al. 2004; Rehmany et al. 2005), and Avr3a from *P. infestans* (Armstrong et al. 2005). While B. Tyler was sorting through predicted proteins with similarity to *P. sojae* Avr1b-1 and comparing these with the other Avr sequences provided by J. Beynon and S. Kamoun, he discovered a common pattern in all the proteins that occurred downstream from the signal peptide. It was truly a eureka moment that electrified the atmosphere in the annotation room at the Joint Genome Institute. The potential significance of the RxLR-dEER motif was immediately recognized, and the discovery created a flurry of new activity.

Now, two years later, all the indicators are that the RxLR-dEER motif is fulfilling its promise as a crucial component of the molecular arsenal of oomycete plant pathogens (Birch et al. 2006; Ellis et al. 2006). The striking similarity of the oomycete RxLR-dEER motif to the *Plasmodium* export element (PEXEL) motif has been duly noted (Rehmany et al. 2005), and recent functional studies support its predicted role as a sequence pattern that targets pathogen proteins for delivery to the inside of host cells (Bhattacharjee et al. 2006). Most known oomycete Avr loci encode effectors with an RxLR-dEER motif, but exceptions to this trend are now emerging (Jiang et al. 2006c; Qutob et al. in press). Analysis of the genome sequences from *P. ramorum* and *P. sojae* uncovered a

huge family of some 700 secreted effector proteins containing the RxLR-dEER motif, or roughly 350 for each genome (Tyler et al. 2006). Zhang and associates (2006, this issue) placed the 350 *P. sojae* genes, named Avh genes, onto the physical map and observed extensive heterogeneity in the distribution of Avr genes. Many regions are devoid of Avh genes, whereas others contain many Avh genes sometimes in clusters. Moreover, Avh genes are often located in regions in which the conserved synteny between *P. sojae* and *P. ramorum* is lost, suggesting that Avh genes are associated with sites of elevated genome fluidity.

Secreted proteins have always been good targets in searches for pathogenicity factors. This topic has just been reviewed in connection with plant-pathogenic oomycetes (Kamoun 2006). New methods can be applied to identify secreted proteins, as illustrated by the study of Lee and associates (2006, this issue). These investigators used a yeast secretion trap (YST) expression system to identify a variety of pathogen (*P. infestans*) and host (tomato) secreted proteins that are expressed during infection. Their work demonstrates the utility of the YST methodology and provides a complement to in silico or computation-based algorithms that rely on EST databases (Torto et al. 2003).

Secreted proteins from *P. ramorum* were also directly measured by extracting cell-wall components and performing mass spectrometry on peptic digests (Meijer et al. 2006, this issue). A total of 17 different secreted proteins that are associated with *P. ramorum* cell walls were identified, including many mucins and glycoside hydrolases (GHs). Some well-known *Phytophthora* proteins were also found: an elicitor, a Kazal-type protein, and two proteins similar to a transglutaminase that has been well-characterized as a pathogen-associated molecular pattern (Brunner et al. 2002). The GHs identified in this study belong to different GH families than the ones recently described by Costanzo and associates (2006). They mined *Phytophthora* databases for the GH12 family, whose members are thought to be targets of xyloglucan-specific endoglucanase inhibitor proteins that are widespread in plants. *P. sojae* and *P. ramorum* both contain a GH12 gene family, 10 and 8 members, respectively, all of which are transcribed in mycelium. All GH12 proteins have a signal peptide but, as yet, their subcellular location has not been determined.

To study the evolution of genomic sections encoding secreted proteins, Jiang and associates (2006a, this issue) selected four regions in *P. sojae* and in *P. ramorum* and performed an in-depth comparative analysis of gene order and conservation between the two species. This showed contrasting patterns of conserved synteny. Whereas gene clusters encoding secreted elicitor proteins were largely conserved in number and order, the organization of genes encoding cutinases and the Avr1b-1 effector protein were substantially different between the species. These differences likely arise from selective pressures imposed by the distinct host plants and environments that the two species inhabit.

The *Phytophthora* molecular toolbox continues to grow.

Phytophthora research has always presented special challenges. These species are chosen for study because of their economic and environmental impact as pathogens and invasive organisms, not because they are particularly suited to laboratory work or genetic investigations. Nonetheless there are an impressive number of protocols and methods worked out for molecular and genetic analyses, especially for *P. infestans* and *P. sojae*. Methods for performing genetic crosses have been crucial to mapping and inheritance studies in heterothallic and homothallic species (Förster et al. 1994; Judelson et al. 1995). The addition of EST and genome sequencing has provided a

wealth of new information for the design of DNA markers. Microsatellites, or simple sequence repeats, from the *P. ramorum* genome sequence are already being deployed to trace the lineage of North American and European isolates of this pathogen (Ivors et al. 2006). Similarly, microsatellites based on *P. infestans* EST and genome sequences are being used for analyzing *P. infestans* populations (Lees et al. 2006).

Papers describing transformation (Cvitanich and Judelson 2003; Judelson et al. 1991, 1993; Vijn and Govers 2003) and gene silencing (Gaulin et al. 2002; van West et al. 1999; Whisson et al. 2005) are available for a few *Phytophthora* species, but these methods often have limitations. The powerful method of mutation screening by targeted induced local lesions in genomes (TILLING) has now been added to the repertoire of molecular biological protocols available for the genus *Phytophthora*. Lamour and associates (2006, this issue) demonstrate that libraries of ethylnitrosourea-treated *P. sojae* cultures can successfully be generated and screened for induced point mutations in target genes. Several mutants were identified for two different genes in *P. sojae*, one encoding a necrosis-inducing protein (*PsojNIP*) and the other a phospholipase D (*PsPXTM-PLD*). A full characterization of these *P. sojae* TILLING mutants still needs to be performed, but the method itself appears to offer a promising alternative to gene silencing. The same group developed a TILLING resource for *Phytophthora capsici*, another important crop pathogen that has the potential to be upgraded as a model for molecular-genetic research on oomycetes (K. H. Lamour, *personal communication*).

Gene naming system proposed.

The number of *Phytophthora* and other oomycete genes that have been characterized has steadily increased over the last 15 years, but there has been no standardized nomenclature system. Genome sequencing has brought this problem to the forefront by creating an avalanche of genes that require naming. At a recent Oomycete Molecular Genetics Network (OMGN) meeting in Wageningen, The Netherlands, H. Judelson outlined a proposal for consistent naming of oomycete genes. Genes would be described by three to seven characters, beginning with letters and followed optionally by a numeral. The full proposal can be downloaded from the Oomycete Molecular Genetics Research Collaboration Network website. Naturally, an agreement on a system for naming genes would be beneficial for all persons interested in the genetics of these organisms and could also make the oomycete literature more accessible to those from other fields.

Phytophthora: An expanding genus that caters to many tastes.

Ever since the first late blight epidemics spread over Europe and the plant destroyer was baptized as the *Phytophthora* genus, scientists of all kinds have laid hands on these organisms. In 1996, Erwin and Ribeiro published a standard book covering many aspects ranging from taxonomy, detection, physiology, and genetics to disease control and supplemented with laboratory protocols and an extensive bibliography. They describe the 64 species and subspecies that were known at that time. Ten years later, we can add at least 18 new species to that list, including *P. ramorum* (Werres et al. 2001), and several natural hybrids that have acquired the ability to exploit new hosts (Brasier 2000). The many existing and newly emerging *Phytophthora* species continue to be a threat to agriculture, but at the same time, they pose a challenge and a resource for scholars in other disciplines.

Evolutionary biologists have been quick to use the *Phytophthora* genome sequences to probe patterns of eukaryotic evolu-

tion. For example, Richards and Cavalier-Smith (2005) use genomic data to propose that the evolution of eukaryotic phyla can be bifurcated into unikont (single flagellum) and bikont (two flagella) lineages (Fig. 1) and that this is reflected in the domain structure and organization of myosin proteins. In another study, genome analysis suggests that pathways of acetate metabolism in *Phytophthora* spp. and *Chlamydomonas reinhardtii* are similar to one another but distinct from fungal species (Ingram-Smith et al. 2006).

The discovery of the similarity in putative host cell-targeting motifs, PEXEL and RxLR-dEER, in organisms at both ends of chromoalveolate spectrum may just be the beginning of an exciting expedition in search of features shared by plant and animal pathogens. In this respect, the comparison between plant and animal pathogens within the oomycete lineage could be even more interesting. EST sequencing of the oomycete fish pathogen *Saprolegnia parasitica* revealed several putative virulence factors with similarities to *Phytophthora* proteins as well as proteins with an RxLR-dEER motif (Torto-Alalibo et al. 2005; van West 2006). Hopefully, the list in Table 1 can soon be extended with species from other oomycete genera.

The self-assembly of a community network.

It cannot be restated enough that a united research community is of crucial importance to make a success out of a genome sequencing project. Reaching consensus about the strain or strains to be sequenced and supplying the sequencing centers with the biological material are just the first steps. Once the sequence is assembled, an accurate manual annotation, based on consistent nomenclature and preferably approved by curators, is another step that should guarantee high-quality genome databases. Web-based interactive annotation platforms rely heavily on the input of many individuals, and the same is true for the development and maintenance of resources for functional genomics.

Within the plant pathology community, phytophthorologists have always created their own networks. The documented history of the first special discussion group focused on the genus *Phytophthora* goes back to the 1960s, to the First International Congress of Plant Pathology in London (ICPP 1986). The *Phytophthora* Newsletter (PN), first issued in 1973, reported on the many workshops and discussion groups, the appearance of new species, protocols and culture collections, and updated the readers on membership directories. Although PN petered out after number 19 in 1993, numerous scientists engaged in many aspects of *Phytophthora* pathology and biology participate in networks or meet in subgroups at larger meetings. In the last 15 years, we have personally experienced how important and stimulating these networks are to develop a cohesive community. When we first entered this field, we attended meetings with a classical pathology signature, such as the ad hoc North American *Phytophthora* meetings organized by C. Grau (University of Wisconsin) or the '*Phytophthora infestans*-150' meeting in Dublin, Ireland, in 1995. These meetings were important in forming a nucleus of scientists interested in genetics and molecular biology of oomycetes. In 1995, the Fungal Genetics Conference in Asilomar started with concurrent workshops integrated in the program. One of the workshops had 'oomycetes' in the title and has become a recurring biennial event. Two years later, Asilomar was the place where the *Phytophthora* Genome Initiative (PGI) was launched and, on the beach, the first plans for EST sequencing were drafted. In June of 1998, a PGI workshop occurred at the National Center for Genome Resources (NCGR) in Santa Fe, New Mexico (organized by B. Sobral and B. Tyler). This meeting was important for the establishment of the NCGR *Phytophthora* web server, now called the *Phytophthora* Functional Genomics database. Two months later, there was a one-day *Phytophthora* meeting in

Edinburgh, Scotland, organized by D. Cooke and P. Birch. This was a satellite of the 7th ICPP and, in the corridors, the foundation was laid for the *Phytophthora* Syngenta Research Consortium (SCRI). This consortium was an enormous boost for *P. infestans* research and oomycete research in general, because it had the financial backing to establish an impressive EST resource, at that time unprecedented for any other plant pathogen (Randall et al. 2005). In 1999 and 2001, S. Kamoun organized meetings at the Ohio State University in Wooster, Ohio, that set the stage for a united oomycete research community with a primary interest in molecular genetics. B. Tyler took the initiative to give the network a more solid and formal status and applied for a research network grant from the National Science Foundation. The last five years this grant was a solid source of funds for the annual network meetings and travel awards for community members, in particular Ph.D. students. The travel awards were not only meant for attending the meetings but also for visiting other labs to learn new techniques and to exchange ideas. The *Phytophthora* Molecular Genetics Network is now renamed the OMGN, and the application for renewal is pending. In May of this year, OMGN met for the first time in Europe (Wageningen, The Netherlands) and, with 85 participants, was the largest meeting in the series and the first one with a significant input from scientists working on animal oomycete pathogens.

Around the globe there are numerous venues for discussion of molecular and genetic research on *Phytophthora* spp. and other oomycetes. Obviously, many of these happenings may be outside of the research networks and meetings that are mentioned here. We have simply provided a short history from our perspective. In any case, the OMGN now provides a regular and open international forum that welcomes new participants.

Since the launch of *Molecular Plant-Microbe Interactions* (MPMI), the journal has been an excellent platform for publishing molecular-genetic research on oomycete plant pathogens. One of the first volumes included a paper on stable DNA transformation of *P. infestans*, which was a major breakthrough in the field (Judelson et al. 1991). In 2000, the MPMI board added a senior editor covering oomycete-plant interactions, reflecting the trend to separate oomycetes into their own niche. We hope that this Focus issue on *Phytophthora* genomics will illustrate to readers of MPMI that there is a lot to learn from oomycetes.

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AUTHOR-RECOMMENDED INTERNET RESOURCES

Community annotation database for oomycetes: phytophthora.vbi.vt.edu
 DOE Joint Genome Institute (JGI) *P. sojae* genome database:
genome.jgi-psf.org/sojae1/sojae1.home.html
 DOE JGI *P. ramorum* genome database:
genome.jgi-psf.org/ramorum1/ramorum1.home.html
 Oomycete Genomics Database (OGD): www.oomycete.org
 Oomycete Molecular Genetics Research Collaboration Network website:
pmgn.vbi.vt.edu/
Phytophthora Functional Genomics database: www.pfgd.org
 Broad Institute *Phytophthora infestans* database:
www.broad.mit.edu/annotation/genome/phytophthora_infestans

Errors in the Lamour et al. 2006 and Meijer and Govers 2006 citations were corrected in the online version on May 10, 2007.