British Naturalists' Association
The National Body For Naturalists
Founded 1905

Phytophthora; what's the Problem(s)

Roy Stewart MBNA FIBMS, FLS, FRSB

There are two main problems that will be highlighted by this article. The first is still the misconception that *Phytophthora* is a fungus and the second will be the current devastation caused by *Phytophthora* and possible future consequences.

Feature	Oomycete	True Fungi
Neighbouring taxonomic groups	diatoms and golden-brown algae	animals
Hyphal architecture	aseptate and coenocytic hyphae	either single cell or septate with one or more nuclei per compartment
Ploidy of vegetative hyphae	diploid except for transient haploid state in gametogenia	Typically, haploid or dikaryotic often with stable diploid state following mating
Typical size of genome	50 - 250mb	10-40mb
Major glucans in cell walls	cellulose and Beta linked glucose polymers	usually chitin and/or chitosan and Beta linked glucans
Pigmentation	usually, unpigmented	very common in hyphae and spores
Toxic secondary metabolites	none described	common; typically, aromatic heterocyclic hydrocarbons
Mating hormones	non peptide and probably lipid like	usually, small peptides and lipopeptides
Predominant asexual spore	undessicated unicellular sporangia	desiccated single or multicellular conidia
Motile asexual spores	nearly universal biflagellate zoospore	uncommon and only found in chytrids which are monoflagellated
Sexual spores	oospores on terminal of specialized hyphae	various types often in large numbers in specialized complex enclosures e.g., fungal cap
Major energy reserves used by spores	mycolaminarin and lipid and possibly polyphosphate	glycogen and trehalose with sugar alcohols and lipids
Mitochondria	internal cristae tubular	internal cristae lamellar
Sterols	phytosterols e.g., fucosterol or cholesterol derivatives	ergosterol
Polarized growth of hyphae	Spitzenkörper (SPK) not present	Spitzenkörper (SPK)present and constitutes a collection of secretory vesicles and polarity-related proteins
Lysine biosynthesis	DAP pathway; also found in algae, plants and bacteria	AAA pathway also found in euglenoids

The table shows features that are used to distinguish fungi from oomycota.

Up till the late 1980s *Phytophthora* was still considered a fungus but since then the evidence has been accumulating to the point that *Phytophthora* has now clearly been reclassified. Unfortunately, it is still often referred to as a fungus forestry report and as recent as last year two new popular albeit non-technical/academic books still called it a fungus and even a referred to it as a fungal pathogen. It's unfortunate that part of its new classification includes the word mycota and it is because of this that they are often described as fungal like.

Phytophthora belong to oomycota. Oomycota comes from the Greek ωόν (oon, 'egg') and μύκητας (mykitas, 'fungus'). This name is derived from the large round oogonia which are the large structures containing female gametes. The other name that is often used is "water mold" and this refers to their preference for conditions of high humidity and running surface water, which is again a characteristic of the oomycetes. A definition that is often used is 'They from a distinct phylogenetic lineage of fungus like eukaryotic microorganisms and characterized by hyphal growth. Again, the problem with this naming is that it implies that the oomycota are fungi. **They are not fungi.** Looking at the tree of life it is clear they now sit within the stramenopiles group along with brown algae, diatoms, dinoflagellates and ciliates and it is obvious they sit a long way from fungi which sit alongside animals to which they are more closely related.

The group used to be known as the kingdom Chromista but because flagella are present during various stages of the life cycle and always includes one straminipilous flagellum and this was considered to be the one feature of such importance that led the author Dick to the naming of the Kingdom Straminipila instead of Chromista. The latin derivative of Straminipilous is *stramen* = straw and *pilus* = hair. Classic flagellum has a 9+2 arrangement of microtubules and when it projects beyond the cell surface it tends to be 'naked' and has been coined Whiplash flagella. In contrast, the straminipilous flagellum is coated in 1-2µm hair like structures and these are called Tripartite Tubular Hairs (TTHs) and has led to the name Tinsel Flagellum. These are crucial in the motility of the zoospores once in the watery environment. The actual number of species of oomycota is unknown but a figure of approximately 1000 been suggested and although mainly saprotrophic many are economically important aggressive algae, plant and animal pathogens.

Examples include the following.

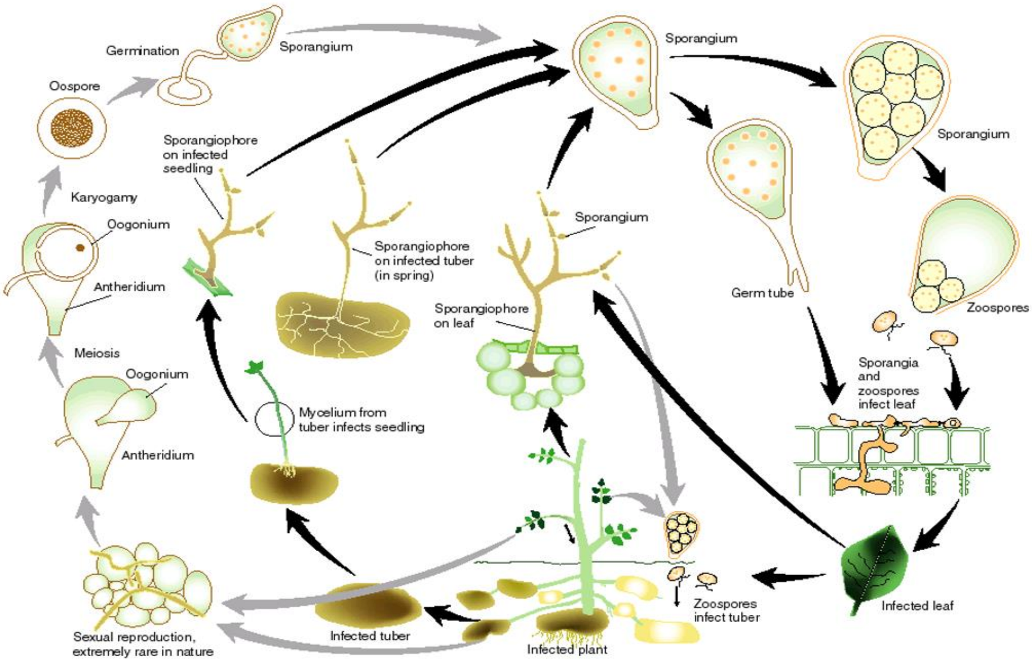
1) *Plasmopara obducens* is an obligate biotrophic pathogen of horticultural plants from the *Impatiens* genus. It causes the *Impatiens* downy mildew foliar disease, which results in wilted and defoliated plants that die within weeks of disease onset (note powdery mildews as opposed to downy mildews are fungal in origin).

2) *Aphanomyces invadans* causes an ulcerative syndrome; It is pathogenic on several economically important fish, including carp, perch and salmonids. It has been responsible for large-scale mortalities of farmed and wild fish in more than 20 countries across four continents.

3) *Saprolegnia parasitica* causes saprolegniosis on various fish species; at least 10% of all hatched salmon succumb. In addition to fish, species of amphibians (could be a global problem) Crustaceans and aquatic insects are also highly susceptible.

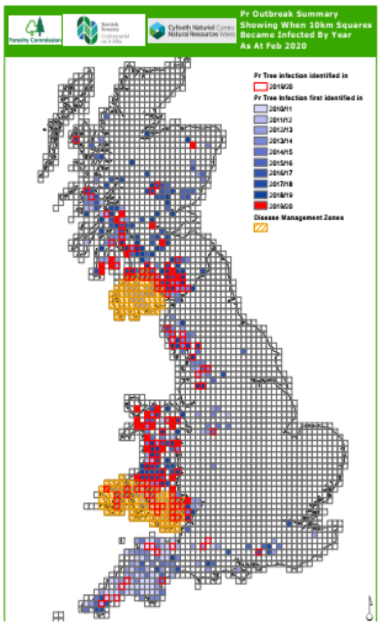
4) *Pythium insidiosum* was considered to be the only oomycete pathogenic for mammals. In 1999 it was reported that several dogs were diagnosed with an unusual oomycete in the genus *Lagenidium* and this was causing extensive cutaneous and subcutaneous infections. The infection has been also reported in humans and cats, and it could possibly affect other mammalian species as well.

Probably the most well-known group of Oomycetes are the genus *Phytophthora.* The name is derived from the Greek and literally means plant destroyer. Currently there are approximately 180 species of *Phytophthora* that have been provisionally named worldwide, with new species being described at an increasing rate as a result of global surveys for *Phytophthora* in an increasing number of environments and it is predicted the number could rise to 500 plus species. There is also the problem of increasing hybridization between species (highlighted later). In Britain, new species of pathogenic *Phytophthora* (eg *P. ramorum, P. kernoviae, P. lateralis, P. austrocedri, P. alni, P. pseudosyringae and P. cinnamomi*) have been reported since 2003, all causing serious damage to trees and plants across a range of different environments and resulting in significant economic and ecological losses. Three of these pathogens (*P. lateralis, P. pseudosyringae and P. austrocedri*) were actually discovered as a result of disease outbreaks on trees at public parks and gardens and all being highly disturbed sites with extensive planting histories. Future invasions of *Phytophthora* from other global sources are likely because of their ability to survive in soil. This raises serious biosecurity issues especially due to the massive importation of plants into this country with very little or only basic monitoring. *Phytophthora* cause numerous problems to plants and often the infection and resulting necrosis may be found in leaves, stems, or roots. If the infection is foliar then it's called BLIGHT. Infection on stems or twigs creates a CANKER which may be localized or expand around the stem. This can lead to a gradual decline or sudden death of the canopy. *Phytophthora* may also invade the water conducting wood (xylem) beneath the inner bark, and cause symptoms in all or part of the canopy associated with water stress, e.g., WILT. It may also invade the phloem causing disruption in the movement of nutrients e.g., sugars. Many *Phytophthoras* infect the roots, causing ROOT ROT; some kill fine roots only, and in others necrosis may progress up the root and into the root crown. Some species can cause multiple symptoms on a single host, or cause different symptoms on different hosts. The problem is many other pathogens, pests, injuries, and abiotic factors may cause similar symptoms therefore correct detection and identification is essential. A quick test in the field can be done with a lateral flow test exactly using the same principles and technique and equipment as used in Covid testing. Again, like Covid to identify a specific species or strain then PCR has to be used. Potato blight is currently the most well-known disease caused by *Phytophthora* and it was a period of mass starvation and disease between 1845 to 1852 and it's estimated about 1 million people died and perhaps up to two million fled the country. The cause of the famine was P. *infestans* and this is fortunately confined only to solanaceous hosts. It also infected potato crops throughout Europe in the 1840s, causing an additional 100,000 deaths. *P. infestans* still causes problems worldwide and huge economic losses. Potato late blight remains a major threat to food security and carries a global cost conservatively estimated at more than $6 billion per year and its estimated the losses would be sufficient to feed anywhere from 80 to many hundreds of millions of people. The genome was found to be considerably larger (240 Mbp) than that of most other *Phytophthora* species whose genomes have been sequenced; eg *P. ramorum* which has a 65 Mbp genome and this may be due to more genes coding for proteins to overcome plant immune defences and proteins involved in plant tissue invasion especially via haustoria.



P. infestans life cycle.
https://www.asiablight.org/what-is-late-blight/

The species of phytopthora that is causing the most concern at the moment is *P. ramorum* which was first found in the UK in 2002, initially in the horticultural trade. *P. ramorum* infects the leaves and shoots of ornamental shrubs such as rhododendron, pieris and camellia. *Rhododendron ponticum* is an invasive, non-native species found in many British woods and forests and unfortunately the infected leaves from *R. ponticum* produces large quantities of spores, putting nearby susceptible trees at particular risk and Since 2009 *P. ramorum* has also been found sporulating on bilberry (*Vaccinium myrtilus*) in heathland. Typical symptoms on rhododendron include leaf blackening, wilted shoots and dieback. Since the mid-1990s, *P. ramorum* has killed millions of tanoak trees and several oak tree species (coast live oak, California black oak, Shreve oak, and canyon live oak), and caused twig and foliar diseases in numerous other plant species, including California bay laurel, Douglas-fir, and coast redwood mainly along the coastal areas of California and Oregon. This has led to the term Sudden Oak Death (SOD). This term (at the moment) does not apply to the UK. The pathogen has been detected on oaks but fortunately does not seem to induce disease but it does however affect Larch trees and causes what has been termed Sudden Larch Death (SLD) in this country. Already 3,000 hectares of larch in Wales, Devon, Cornwall, Somerset and Northern Ireland are known to be infected and thousands of trees have been felled in Scotland especially in Dumfries and Galloway district in an industry worth one billion pounds. The problem is so chronic in Scotland that the area has effectively been sealed off with very strict biosecurity arrangement for felling transport and disposal. The area has also been declared untreatable and the best option is containment as much as possible There are isolated infections in other parts of Scotland but these are now treated On an emergency cull basis. The big potential problem is *P. ramorum* has host range of more than 150 plant species. European Sweet Chestnut (*Castanea sativa*) is also a host, and increasing numbers have been found affected in southern England



The UK outbreak map shows where *ramorum* disease has been confirmed or presumed in larch trees.
https://www.forestresearch.gov.uk/tools-and-resources/fthr/pest-and-disease-resources/ramorum-disease-phytophthora-ramorum/

since 2015. Other conifer species such as Douglas Fir (*Pseudotsuga menziesii*), Grand Fir (*Abies grandis),* Noble Fir (*A. procera),* and Western Hemlock (*Tsuga heterophylla*) can be infected when growing near infected larch. It has also been confirmed on a small number of Sitka Spruce (*Picea sitchensis*), another commercially important conifer species widely grown in the UK.

P. kernoviae was first found in the UK in October 2003 in a large bleeding canker on a mature beech tree in Cornwall. About the same time scientists from the Central Science Laboratory isolated an identical new organism from established rhododendrons, also from South-West England. It was confirmed as being the same organism. The scientist who discovered it was Professor Clive Brasier; he named it *Phytophthora kernovii* after Kernow, the Cornish name for Cornwall, where it was first identified. The spelling was later changed to *kernoviae.* Since then, it has also been found elsewhere in Great Britain, mainly in South-West England, but occasionally at other locations in England as well as Scotland and Wales. The symptoms are very similar to *P. ramorum* so very specific identification is needed.

Phytophthora alni was first discovered in Great Britain in 1993 and is now considered widespread and the estimated number of alder trees affected is now at least 20% with the highest incidence of the disease incidence is in South-East England. Heavy tree losses are also occurring in alder populations in the borders region of Wales and alders on Scottish river systems are suffering damage. Alder dieback is now in 11 European countries including Austria, Belgium, France, Germany, Hungary, Ireland, Italy, Lithuania, Netherlands and Sweden. A sub-species of the organism, called *P. alni* subsp. *uniformis*, has been found in Alaska, and another new *Phytophthora* has been reported affecting alder trees in Australia. *P. alni* can infect all species of alder, including the UK's native common or black alder (*Alnus glutinosa*) and the other two species widely planted here, which are Italian alder (*A. cordata*) and grey alder (*A. incana*). Green alder (*A. viridis*), another species native to continental Europe, but less often used here, is also susceptible. It appears to be highly specific to alder species, and is not known to affect plants in any other genus. Common alder in particular has considerable landscape value along waterways; it plays a vital role in riparian ecosystems and the root system helps to stabilise riverbanks. Molecular analysis has shown that *the P. alni* is a hybrid between *P. cambivora* and *P. fragariae* like species – a pathogen of strawberry and It is now spreading across Europe as a hybrid swarm. Some of the hybrid types are locally very damaging, and pose a serious threat to alder. The standard type of the pathogen has recently been named as *Phytophthora alni subspecies alni*, and is the most aggressive variant. The different hybrid types or variants are collectively known *as P. alni subspecies uniformis* and *P. alni subspecies multiformis.* The species consists of a range of heteroploid organisms and includes *P. alni* subsp*. alni* which is a tetraploid, while *P. alni* subsp. *uniformis* and *P. alni* subsp. *multiformis* have chromosome numbers between a diploid and a tetraploid.

P. lateralis is thought to originate in Asia. It is now the main cause of death of Lawson cypress trees in their native range in the West Coast region of North America but the pathogen was also first discovered in the UK in 2010, at Balloch Castle Country Park in West Dunbartonshire, Scotland. Since then numerous Infection sites have been identified and now include forest stands, windbreaks, parks and private gardens. The most likely source of the outbreaks in the UK has been the importation of infected plants from neighbouring European countries – four confirmed outbreaks on mature trees in the UK have been on nursery sites or next to garden centres or plant sales areas. Outbreaks of infection have been confirmed in Lawson cypress trees in South-West England, Yorkshire, Scotland and Northern Ireland. The disease is most prevalent on the western side of Central Scotland. Although *P. lateralis* mostly affects Lawson cypress trees its host range also extends to: Sawara cypress (*Chamaecyparis pisifera*);western red cedar (*Thuja plicata*);Pacific yew (*Taxus brevifolia*), a close relative of Britain's native common yew (*T. baccata*);northern white cedar (*Thuja occidentalis*);other cypress species (members of the Cupressaceae family)juniper (species in the Juniperus genus), periwinkle (Vinca spp.) and petunia (Petunia spp.).Alaskan cedar (*Cupressus nootkatensis*) and Douglas fir (*Pseudotsuga menziesii*) have been found to be susceptible in experimental conditions. It has also been found in soil in nurseries associated with cyclamen, marigold and pomegranate.

P. austrocedri was first isolated in 2000 in a nursery in Germany on creeping Juniper and in 2007 it was discovered to be the cause of dieback and deaths of Chilean cedar (*Austrocedrus chilensis*) in Argentina and the species was fully characterized from this infection. In Scotland it has infected amenity specimens of Lawson cypress (*Chamaecyparis lawsoniana*) and Nootka Cypress (*C. nootkatensis)* and a Mediterranean cypress in Iran. Although Juniper is protected it was already recognised as vulnerable in Great Britain before *P. austrocedri* was confirmed here. Figures from Natural England report that of 35 SSSIs in England where juniper is a main feature, 66% are in unfavourable condition and since 1990 onwards the extent of Juniper and its condition has declined considerably, especially on upland sites, where its importance is tied in with nature conservation and game management. Overgrazing, burning, deforestation, lack of regeneration and other land-use changes are factors mainly causing its decline but *P. austrocedri* infection could accelerate this decline.

P. pluvialis is known to affect a variety of trees including western hemlock, tanoak, pines and Douglas-fir. It was originally reported in Oregon, USA in 2013 on tanoak and Douglas fir and was subsequently identified as the pathogen responsible for 'red needle cast' of radiata pine in New Zealand. Of great concern is *P pluvialis* was discovered in a woodland in Cornwall in September 2021, where it was found to be affecting mature western hemlock and Douglas-fir trees.

As of writing **This is the first report of this pathogen in Europe**. It's currently under investigation to see if it's actually the cause of the disease or a 'passenger' but it's thought to have been in Britain for more than 100 years. Although it is often found on ornamentals including shrubs, increasingly it has been found to affect trees such as sweet chestnut and oak, attacking the roots and root collar. The disease it causes on sweet chestnut is known as ink disease because of the blackish colour of infected roots and associated soil.

Overall devastation in Bagger Woods, Barnsley

P. cinnamomi is distributed world-wide and causes disease on hundreds of hosts, including azalea, rhododendron, camellia, boxwood, eucalyptus, avocado, pine, juniper, hemlock, spruce, fir, cedar, and cypress. The disease is very promiscuous and infects economic groups as well, including food crops such as avocado and pineapple. Research has shown that *P. cinnamomi* can infect club mosses, ferns, cycads, conifers, rushes, grasses and lilies and a large number of species from many dicotyledonous families. In the South-West Botanical Province of Western Australia (WA), an estimated 40% of the 5710 plant species, are susceptible to *P. cinnamomi,* including 14% considered highly susceptible. This could be the most dangerous species of all *Phytophthora.*

Effect on pine needles

What does the future hold? A couple of recent studies could highlight future problems we could face. Metabarcoding is a powerful technique that enables the identification of multiple species present in a single environmental sample based on a DNA 'barcode' unique to each species. A study in Scotland (Green et al 2020) using this technique found 23 *Phytophthora* species, the majority of which are known to be pathogens of woody hosts and were detected across all sites sampled. These included nineteen of the forty-two species recently listed as present in the UK and four species not previously recorded in Britain. Also detected were three as-yet undescribed *Phytophthora* species and nine oomycete sequences with no clear match to any known genus. Another study (Riddell et al 2019) used the same technique to analyse *Phytophthora* species diversity in soil samples collected from fourteen public garden/amenity woodland sites in Scotland. A high diversity of *Phytophthora* s was detected at all sites, corresponding overall to 23 *Phytophthora* species as well as twelve as-yet undescribed oomycete sequences. The question is: will these new species become pathogenic. Nobody knows but very careful surveillance and rapid action could possibly restrict their effect on what's becoming a global problem. The future is not looking very bright at the moment.

Effect on bark

Black bleeding lesions

All photos: R. Stewart

References

Everett M. Hansen. *Phytophthora* Species Emerging as Pathogens of Forest Trees. Curr Forestry Rep (2015) 1:16–24

Gordon W. Beakes & Sally L. Glockling & Satoshi Sekimoto. The evolutionary phylogeny of the oomycete "fungi". Protoplasma (2012) 249:3–19.

Burki et al., The New Tree of Eukaryotes, Trends in Ecology & Evolution 2020 Jan;35(1):43-55.

McGowan J, Fitzpatrick DA. Recent Advances in oomycete genetics. Adv Genet. 2020;105:175-228

William Fry. *Phytophthora* infestans: New Tools (and Old Ones) Lead to New Understanding and Precision Management. Annu Rev Phytopathol 2016 Aug 4;54:529-47.

Chepsergon et al. Organize, Don't Agonize: Strategic Success of *Phytophthora* Species. Microorganisms. 2020 Jun 17;8(6):917.

Suomeng Dong and Wenbo Ma. How to win a tug-of-war: the adaptive evolution of *Phytophthora* effectors. Curr Opin Plant Biol. 2021 Aug;62:102027.

Roy Stewart is Chairman of South Yorkshire branch and a BNA Trustee. This article was originally a PowerPoint talk given by Roy through an online Zoom portal for the BNA National AGM on 6th October 2021. It was reproduced as an article in the Country-*Side* Summer 2022 issue, and has since been adapted into a web article.