T5.11: Review: Case Study of *Phytophthora Ramorum*, an Emerging Plant Pathogen in Cultivated and Wild Environments

Alison J Wright and James Woodhall
Plant Health Group,
Department for the Environment, Food and Rural Affairs

Abstract:

Phytophthora ramorum emerged as a plant pathogen in the 1990s. It came to prominence as the cause of 'sudden oak death', a tree disease in western North America but has the ability to infect a broad range of plant species. In Europe, it has mainly affected ornamental species, *Rhododendron, Camellia* and *Viburnum*, and in the wild occurs predominantly in the rhododendron understorey and on a limited number of associated trees. *P. ramorum* thus has an economic cost through plant losses in horticulture and forestry and also an impact on the environment. It causes a range of symptoms including leaf blight, stem dieback, bark canker, all of which may result in plant death. Recently developed molecular methods which can be deployed 'on site', at nurseries or ports, ensure rapid diagnosis and assist in the implementation of EC legislation aimed at controlling the movement of susceptible plant material into/within the EU. Long distance spread of the disease has been through international trade in plant material. Local spread by water, aerial spores and soil movement has been demonstrated. The impact of the disease may increase with the emergence of more aggressive strains through hybridisation or through climatic changes producing more optimal conditions for the pathogen.

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Introduction

Phytophthora ramorum is the causal pathogen of sudden oak death, a disease that owes its name to the extensive tree mortality it causes, which was originally limited to native American oaks on the Pacific west coast of the United States. But today, *P. ramorum* is causing problems on both sides of the Atlantic. Its multi-host nature means that, in addition to an ever-growing list of tree species being infected, the horticultural trade is also suffering, as the pathogen is able to infect many ornamental plant species, most notably *Rhododendron*, *Viburnum* and *Camellia*. Almost uniquely for a plant pathogen, *P. ramorum* is affecting both horticultural and wild environments and therefore poses particular economic and environmental problems. It is under statutory control in the UK and EU. Emergency EC phytosanitary legislation introduced in November 2002 (Decision 2002/757/EC, as amended) included controls on the introduction of susceptible hosts into the EU and also on the movement of the main hosts of *P. ramorum* within the EU. This legislation is subject to review to take account of new developments in the occurrence of the pathogen and in scientific knowledge of it.

This review describes the drivers, sources and pathways that have led to the disease becoming one of the foremost plant health problems faced today in North America and Europe. The role that detection and identification take in managing the disease risk is also presented here, along with an examination of the role diagnostics has played, or should play, in mitigating risk. And key aspects of the pathogen, the diseases it causes, and a summary of current understanding are also included.

Causal agent and biology

P. ramorum belongs to a group of organisms known as the Oomycetes. This group contains many important plant pathogens such as *Pythium* species and downy mildews. Of most notoriety within the Oomycetes is *Phytophthora infestans*, the causal agent of potato blight, which led to the Irish potato famine in the 19th century. Today, *P. infestans* still causes significant crop losses and considerable expense is devoted to pesticides used to control the disease, as discussed by Hardwick in the companion paper to this one.

The Oomycetes are a unique group of pathogens. They were previously classified as fungi and possess several features that are characteristic of fungi, such as spores, hyphae, indeterminate growth and a lack of chlorophyll. However, sequencing of the ribosomal DNA internal transcribed spacer region in the early 1990s confirmed that they had algal ancestry (Förster et al. 1990). Presently the Oomycetes are placed in the kingdom Chromista, a kingdom that also contains several algal groups.

Another trait of *Phytophthora* species that derives from their algal ancestry is that water is key to their lifecycle. Humid conditions are often essential for infection to occur and for disease to develop, and water is often needed for propagules of the pathogen to move to new infection sites. Most *Phytophthora* species are water-borne (e.g. via rain-splash) or soil-borne pathogens for all or part of their lifecycle. *P. ramorum* is no exception. However, unlike most *Phytophthora* species that are pathogens of roots, *P. ramorum* is an aerial pathogen that directly infects the leaves, shoots or bark of its hosts. *P. ramorum* is also able to infect a wide range of hosts, from ornamental plants to forest trees, and causes diseases that include leaf blights, diebacks and complete plant mortality.

Perhaps fundamental to its success as a pathogen is the ability of *P. ramorum* to produce different types of spores. These spores include sporangia, which are typically found on the leaves of hosts such as rhododendron or Californian bay laurel. Sporangia are dispersed locally through rain-splash or wind-driven rain. They can either germinate directly to produce hyphae, which then infect host tissue directly, or release free-swimming zoospores. Zoospores possess flagella and are motile in water, enabling them to find infection sites on host tissue. A further spore type, the chlamydospore, is relatively long-lived and is thought to be capable of surviving harsh environmental conditions. It is regarded as being responsible for *P. ramorum*'s long-term survival, since thick-walled, sexually produced oospores are currently unknown for *P. ramorum* in nature.

Oospores are produced when the pathogen completes its sexual cycle. They are important in generating genetic diversity. *P. ramorum* is heterothallic and so production of oospores requires the presence of two mating types. As in other *Phytophthora* species, these mating types are designated A1 and A2. Currently, oospores of *P. ramorum* have not been observed in nature and have been difficult to produce in the laboratory, both by using A1 isolates belonging to the European population and A2 isolates of the North American population, and with ‘tester’ strains of other *Phytophthora* species. Consequently, there is still some doubt about whether *P. ramorum* has a functional breeding system.

The original analysis of *P. ramorum* populations indicated that almost all isolates from the European population belonged to the A1 mating type, while isolates from woodlands in North America were A2. These populations differ in certain measurements of pathogenicity. For example, European isolates are considered more aggressive to tree bark than American isolates. European isolates are also faster-growing and less variable in growth rate than the American isolates. DNA analysis also confirmed that the populations on the two continents are genetically as well as phenotypically distinct (Brasier 2003). DNA profiling techniques (including AFLP and microsatellite analyses) have indicated that the European and American populations are genetically distinct, with what could be termed an American and a European lineage. The American lineage has been determined to be less genetically diverse than the European one.

Since the original analysis, there have been some instances of potential intermixing of the two mating types. In 2003, A1 isolates were found on ornamental hosts at nurseries in North America (Hansen et al. 2003). A single isolate of the A2 mating type has now been isolated from viburnum in Belgium (Werres and De Merlier 2003). DNA profiling indicates that the A1 isolates found in North America are actually of the European lineage and could be considered a recent introduction via the nursery trade, although there is no direct evidence to confirm such an introduction. DNA profiling also showed that the single A2 isolate and all the A1 isolates found in Europe all belong to the European genetic lineage. The intermixing of mating types could theoretically allow individuals in the populations on both continents to complete the sexual cycle, thereby increasing the genetic diversity of any given population.

Hosts and symptoms

At present, *P. ramorum* has been recorded worldwide to have naturally infected at least 100 different species representative of over 50 different genera, including both tree and ornamental plant species. Laboratory studies have determined that many other plants are also susceptible to infection by *P. ramorum*. It causes various disease types depending on the host. Some plants exhibit only leaf blight symptoms (‘ramorum leaf blight’), with stems and shoots unaffected, for example, ash, Californian bay laurel and *Leucothoe* species. Other plant species suffer dieback (‘ramorum dieback’) due to the leaves, stems, or both, being infected, such as rhododendron, viburnum and holm oak. Some tree species suffer mortality as the result of bark infections of the main stem or trunk. This is called ‘ramorum bleeding canker’ and affects a number of species including beech, tanoak, and coast live oak. Of these trees, some only support bark infections (e.g. beech, coast live oak), while others can support both leaf and bark infections (e.g. tanoak). Rhododendron is the most important foliar host in woodland outbreaks in Europe. Infected trees (beech and oak) have, to date, been found only in close proximity to infected rhododendrons. In the US, the key foliar hosts producing inoculum for epidemics of tree mortality are Californian bay laurel (*Umbellularia californica*), Pacific rhododendron (*Rhododendron macrophyllum*) and tanoak (*Lithocarpus densiflorus*). The main hosts affected in nurseries in Europe have been species of *Rhododendron*, *Viburnum*, *Camellia* and *Pieris*.

On tree species such as beech and oak, the disease causes bleeding stem cankers that are the result of *P. ramorum* infecting and killing the cambium and phloem within the bark. In the USA, cankers over 2m in length and up to 20m above the soil line are not infrequent (Rizzo et al. 2002). A dark-coloured tarry substance oozes from the affected bark. Foliage of infected trees can turn from a healthy green colour to brown over a period of several weeks, and hence the name 'sudden oak death'. However, this name is misleading as the onset of symptoms is not always sudden, affected trees are not always oak, and tree death is not automatic. Consequently, 'Phytophthora canker' has been suggested as an alternative name for this form of the disease (Rizzo et al. 2002).

The Defra plant health website (www.defra.gov.uk/planth/) has an up-to-date host list and an information sheet on *P. ramorum*, which provides further details and photographs.

An economic and environmental threat

The broad host range of *P. ramorum* includes both tree and non-tree hosts, with outbreaks affecting both cultivated (e.g. nursery) and wild (e.g. woodland) environments. There is potential for large socioeconomic and environmental impacts. With respect to epidemics that have occurred in the US, there has been loss of wildlife habitats, food sources and woodland recreational areas in forest ecosystems associated with high levels of *P. ramorum* tree infections. Such epidemics also enhance the risk of forest fires (as a result of infected, dead trees), accelerated water runoff, soil erosion and sedimentation, and they endanger certain plant species. There are also high costs to the timber industries. Control strategies, or fire prevention, and health and safety are also expensive. They include the cost of removing dead trees, which can vary according to their remoteness. As well as woodlands, heathland habitats are also potentially at risk. Tests show significant susceptibility in some heathland species, e.g. bilberry (*Vaccinium myrtillus*) and heather (*Calluna vulgaris*) (A.J. Inman, personal communication).

In Europe, a few woodland outbreaks have occurred, which have primarily affected the rhododendron understorey, with only a few trees being found with bleeding bark cankers. So far, no epidemics of tree mortality, with the associated high socioeconomic and environmental impacts mentioned above, have developed. This is in contrast to the US, where extensive tree loss has occurred in forest epidemics (Knight 2002; Rizzo et al. 2002).

In Europe, *P. ramorum* infections have been found mainly on ornamental nursery stock. Because *P. ramorum* is a notifiable pathogen under EC/UK plant health legislation, eradicatory action must be taken. This involves costs as a result of the direct loss of plant stock and of the disruption of trade during a subsequent quarantine holding period. There is also the cost of maintaining official control such as surveillance, eradication, and containment. A full cost–benefit analysis has not been performed but the estimated costs of official control associated with eradication, containment and surveillance are likely to be small relative to the social, environmental and economic benefits of forests, woodlands, heathlands etc. (Sansford et al. 2004).

Emergence: a brief history of the occurrence and control of the pathogen

The pathogen was first reported in Europe in 1993, when it was observed that an unknown and unidentified new species of *Phytophthora* was the cause of dieback on rhododendron and viburnum in Germany and the Netherlands (Werres et al. 2001). Meanwhile, on the other side of the world, large numbers of native American oak trees in California were observed to be succumbing to a complex set of symptoms that became increasingly referred to as ‘sudden oak death’. By 2000, a *Phytophthora* species had been isolated from the affected bark of these trees. It was identified as being the same *Phytophthora* species as occurred on the rhododendron and viburnum in Europe. Since then, the pathogen has been found on numerous hosts in Europe and North America. In February 2002, *P. ramorum* was found for the first time in the UK on *Viburnum tinus* (Lane et al. 2003) and it was subsequently found on several other ornamental plant species. Despite these findings, the pathogen was still not considered to be present in European woodlands in mid-2003. But by late 2003, *P. ramorum* was discovered in individuals of two tree species in the UK. A bleeding canker was discovered in October on an American southern red oak tree (*Quercus falcata*) (Brasier et al. 2004a) and, a month later, foliar infection was observed on *Castanea sativa* (sweet chestnut) (Denman et al. 2005). Bark infections of beech (*Fagus sylvatica*), horse chestnut (*Aesculus hippocastanum*) and sycamore (*Acer pseudoplatanus*) have followed, as have foliar infections on holm oak (*Quercus ilex*), ash (*Fraxinus excelsior*) and yew (*Taxus baccata*). American northern red oak (*Quercus rubra*) trees with bleeding bark cankers have also been reported in the Netherlands.

Since the first UK outbreak on viburnum, over 500 outbreak sites in the UK have been recorded to date (August 2005). The majority of these sites are in nurseries but a small number are in natural or semi-natural situations. The south-west and west of the UK have been the regions for a particularly large number of outbreaks and it is thought that the relatively mild, wet and humid climate may be particularly conducive to infection and disease development.

Legislation to control *P. ramorum* has been implemented in the EU. Its main aims are the eradication of the pathogen when found in nurseries and to ensure freedom from *P. ramorum* in plants moved in trade by the use of plant passporting controls. These controls apply to plants of the main species susceptible to *P. ramorum* moved within and between EU member states. These movement controls are supported by a comprehensive official inspection regime covering both commercially traded plants and more general surveys of plants in the wider environment. There are also import controls on plant material from third countries, with an area freedom requirement for susceptible plants and wood imported from the US. Full details of the EC phytosanitary measures are presented in the Annex.

In the US, there is a nationwide federal quarantine regulation to prevent the further spread of *P. ramorum* out of affected states, but states vary in the eradication action they apply. In California, the pathogen is considered too well established in woodland to warrant attempts at eradication. Instead, effort has gone into preventing its spread. In Oregon, when the disease was discovered in July 2001 (Goheen et al. 2002a), an eradication campaign involving the removal and burning of infected forest areas was quickly organised (Goheen et al. 2002b). Oregon has now adopted a '*P. ramorum*-free' certification programme for nurseries and is continuing *P. ramorum* quarantine measures, including the eradication of woodland outbreaks in the south-west corner of the state (Hansen and Sutton 2005).

Drivers, sources and pathways

1 Drivers

What has driven the emergence of *P. ramorum* as a major threat to plant health? A paper by Anderson et al*.* (2004) analyses the drivers for the emergence of plant disease and places them in four categories. They are 'pathogen pollution', climate change, agricultural (or horticultural) change and host-parasite evolution.

'Pathogen pollution', a term used to describe the human-mediated movement of pathogens outside of their natural range, is considered to be the major driver for the emergence of plant diseases in general. It is also likely to be the main driver for *P. ramorum* through the international trade in plants and plant products, including wood from the (presently unknown) centre or centres of origin of the pathogen. It is known that *P. ramorum* is capable of being introduced into countries by the trade in ornamental plants (Stokstad 2004; Pain 2004). The recent emergence of *P. ramorum* in Europe and North America may also be linked to the increasing demand for exotic plant species for amenity and horticultural purposes (Perrings et al. 2005). This demand has resulted in new trade routes, and one such route could have been established with the area of origin of *P. ramorum*.

Of the other drivers mentioned by Anderson et al*.* (2004), host–parasite evolution may also have played a part in the emergence of *P. ramorum* by allowing it to adapt to infect new hosts that are economically important in international trade. Pathogen pollution, through the international trade in already infected plants, would then have played a role in this host–parasite evolution process by the introduction of new hosts. There are little or no data available to test the validity of this hypothesis. But a very real potential host–parasite evolution scenario would be presented by the bringing together of the two populations and mating types of *P. ramorum.* As detailed earlier, European isolates are predominantly of the A1 mating type, while isolates from the North American population are predominantly of the A2 mating type. Genetic recombination through sexual outcrossing of A1 and A2 isolates would be a driver for the evolution of *P. ramorum*, and would probably lead to an increase in pathogen fitness (Brasier 2003). The likelihood of such sexual outcrossing is under debate, given that, when A1 and A2 isolates are brought together in culture, it appears that the breeding system is not fully functional (Brasier et al. 2005a). However, somatic recombination could occur via a fusion of zoospores between different populations (Brasier 2003). The increase in the total genetic diversity of the pathogen population generated by such sexual or somatic gene flow could allow greater potential for the development of resistance to pesticides and for overcoming host resistance, both of which would increase the risk posed by *P. ramorum*.

The finding of A1 isolates possessing the 'European genetic lineage' in North American nursery stock could indicate that pathogen pollution – in the form of trade in nursery plants – may have already acted as a driver to bring the European and North American genetic lineages together. Recently, one study reported an isolate from a Washington nursery which the authors postulate, based on their genetic and morphological analysis, could be an A1/A2 recombinant or even an isolate representative of a third, as yet unknown lineage (Garbelotto et al. 2005).

Future host–pathogen evolution may involve hybridisation between indigenous *Phytophthora* species and the newly arrived *P. ramorum*. Natural hybridisation in Oomycetes is thought to be rare but there have been reports of it within the *Phytophthora* genus, such as the species hybrid responsible for a recently reported disease of alders (Brasier et al. 1999).

The continuing and increasing demand for exotic plant species for amenity and horticultural purposes (Perrings et al. 2005) is an important driver of horticultural change. With regard to climate change, *P. ramorum* is regarded as a cool-temperate organism and, from current outbreak data, it does appears to thrive in cooler, wetter climates. Research in both the US (Davidson et al. 2005) and the UK (J.A. Turner, personal communication) has indicated that a hot, dry spell has the effect of suppressing the organism. It then survives as leaf infections on evergreen hosts and activity occurs again in the wet winter and spring months. The main driver is the mild, wet weather. Any long-term climate change that results in milder, wetter winters will therefore be important in promoting disease development, while any change that results in the loss of hot, dry spells in the summer is likely to augment the spread of the disease.

2 Sources

P. ramorum has been detected in both the North American and European continents. It is possible that there has been some very recent movement of the populations of *P. ramorum* between the two continents since isolates of the European genetic lineage have been found on nurseries in the US, although it must be emphasised that no trade link has been established. However, given the presence of the different mating types and populations in the two continents it is highly likely that *P. ramorum* was independently introduced to both regions and occurs naturally (with both mating types present) in one or more, as yet unknown, country or countries of origin.

One possibility is that *P. ramorum* evolved in an Asian ecosystem. It is genetically similar to other *Phytophthora* species that originate in Asia. An alternative hypothesis is that *P. ramorum* might have evolved as a pathogen of *Rhododendron* or other Ericaceae. The centre of origin for *Rhododendron* is the Himalayas and south-east Asia. *Viburnum* is also found in this region. One could postulate that the pathogen may have been introduced from such an area on imported ornamental *Rhododendron* or *Viburnum* species. There has been both commercial trade and the movement of private collections of rhododendron from these areas for some time. Regions such as the Himalayas and the Yunnan province in south-west China have been highlighted specifically in this respect (Brasier et al. 2004b). Equally, because of the common susceptibility of *Rhododendron* to *Phytophthora* species in general, the *Rhododendron* pathogen theory could be considered a red herring, and *Rhododendron* may act only as a carrier of the pathogen via the nursery trade (Sansford et al. 2004).

Determining the origin of *P. ramorum* will be important in combating the disease. Legislation could then be introduced to halt the movement of plants (and hence the pathogen) from this area. In addition, plants in the site of origin have co-evolved with the pathogen, thereby developing defences against *P. ramorum* infection. The determination of which factors hinder the progress of the disease in its natural environment might facilitate development of control measures elsewhere.

International trade in ornamental plants is postulated as the main driver for the emergence of *P. ramorum*. It also presents a potential threat as a source of the disease. This risk has been addressed in EC and national legislation by the introduction of phytosanitary measures on susceptible material traded both into the EU from non-EU countries and within the EU. The measures involved give assurances that plant material is free from *P. ramorum*. Details of these measures are given in the Annex. Since these phytosanitary measures have been introduced, there has been a marked reduction in the incidence of infection on plant-passported material. There was a drop of almost 90% in findings in 2004 compared to 2003 (Defra plant health website: www.defra.gov.uk/planth/).

However, the risk remains that, because phytosanitary measures do not apply to all known hosts, there will be undetected imports or movement of infected material into and within the EU. To determine the extent of this risk, the Defra Plant Health and Seeds Inspectorate (PHSI) has carried out additional checks at ports in England and Wales on lorries bringing plants from the continent. Over 1,000 inspections of such material in 2004/05 produced no positive findings of *P. ramorum*. The results are encouraging, suggesting that the current measures are reducing the risk. These inspections are continuing alongside routine monitoring by the PHSI of non-passported species in nurseries. There is a need to be vigilant as new hosts are still being found and there is a growing list of experimental hosts that, as they have not yet been found naturally, cannot be listed in legislation. Significant among these is bilberry (*Vaccinium myrtillus*), which, in laboratory tests, has been shown to be both highly susceptible and to have the potential to produce significant numbers of sporangia (A.J. Inman, personal communication). This is an important species in UK heathland and as an understorey species in certain woodlands that grow on acidic soil.

The EC eradication measures are aimed at plants moving in trade. For findings of the pathogen in natural or semi-managed woodlands, there is a general requirement to 'take appropriate measures to at least contain' *P. ramorum*. This containment policy means that there are now, in some countries, known foci of infection that are not being eradicated. These could fuel local epidemics, particularly if significant numbers of infected sporulating hosts such as rhododendron are present. There is strong evidence to suggest that epidemics in Californian oak forests have been driven by the presence of sporulating foliar hosts such as the Californian bay laurel and tanoak. Similarly, the recent findings of cankers on mature established trees in managed woodlands in the south-west and south-east of England are all associated with high numbers of infected rhododendron, which, as a foliar sporulating host, almost certainly acted as the inoculum source for these trees. Rhododendron is an evergreen foliar host and as such can be a significant source of inoculum: the pathogen is able to survive over the winter months through both leaf and shoot infections and can produce significant numbers of infectious spores when favourable conditions resume.

The eradication of *P. ramorum* in woodland areas has already proved difficult in Europe. It is hard to clear the understorey of rhododendron (and to prevent regrowth), and other sources of the pathogen such as leaf litter, soil and water courses are equally, if not more, problematic to subject to an eradication programme. In the Netherlands, eradication in such areas is no longer attempted because of these difficulties, although containment measures are applied, as required under EC measures. In the UK, eradication programmes have been introduced in the few small managed woodlands so far found to be affected. Given these factors, *P. ramorum*-affected woodland areas in Europe could act as reservoirs for the pathogen. There would then be a risk of infectious particles, including both spores and infected material, dispersing from the site via a number of pathways (see below) to further susceptible hosts in woodland or nurseries.

3 Pathways

In considering the pathways through which *P. ramorum* and the diseases it causes spread, it is important to look at both long- and short-distance dispersal.

Long-distance dispersal. The international trade in plants and plant products is a major means by which *P. ramorum* arrives in new areas and spreads once it reaches them. It is the main pathway for long-distance spread of the pathogen, which is carried on foliage and stems and also in the associated growing medium. Transport technology has developed and now allows faster journey times under refrigerated conditions. This allows plants, and also their associated pathogens, to reach their destination in good condition(Ebbels

2003). Trade in plants is a significant pathway both between and within countries. The increasing movement of plants from a central depot to many retail centres throughout a country, and their subsequent distribution in the retail trade, poses a very real risk for the medium- to long-distance spread of the pathogen. The long-distance spread will primarily be effected through the international trade of ornamental plants that have infected foliage, but may also occur through the movement of contaminated growing media and mulches, diseased cut bark and wood as logs or sawn wood. The inoculum load of the pathogen on bark and wood is likely to be less. Of the tree hosts on which the disease has been observed to date, little or no sporangial sporulation has been detected on the trunk.

Potential factors increasing the risk of long-distance spread through the trade in plant material include the presence of undetected long-lived spores and the use of fungicides that mask symptoms.

P. ramorum readily produces relatively long-lived chlamydospores, which are likely to survive in the soil independent of a host (for details, see ‘Causal agent and biology’ above). These long-lived spores, together with sporangia and zoospore cysts, will be significant in the risk posed by long-distance spread if they are moved through soil attached to boots or vehicles, or in the growing media of plants moved in trade (Linderman and Davis 2005). Oospores, another long-lived spore, may also pose a similar risk if sexual reproduction between the A1 and A2 mating types is found to occur naturally.

The widespread commercial use of fungicides, many of which inhibit fungi rather than killing them, has been suggested as a possible factor that allows the dispersal of *Phytophthora* species in infected but symptomless ornamental plants or in their growing medium (Brasier and Jung 2003). This, along with the variation in asymptomatic infection between species and cultivars of ornamental hosts, may already have increased the risk of spread of *P. ramorum* in both of the affected continents as well as to other locations.

This risk has been addressed in a revision to the original EC legislation. There is now an additional requirement in cases where *P. ramorum* has been found at places of production. Where this occurs, for all susceptible plants within a 10m radius of infected plants and any remaining plants from the affected lot, no treatments that may suppress symptoms of *P. ramorum* may be carried out for three months after eradication measures have been taken when the plants are in active growth. This requirement should reduce the risk of asymptomatically infected hosts being moved in trade.

Local dispersal. Local dispersal occurs principally through rain-splash of sporangia. Sporangia are directly infectious but also germinate to produce zoospores that possess flagella and are motile in water films. Studies have shown that rainwater can disperse the inoculum by at least 10m (Davidson et al. 2005) during wind-driven rain events (Davidson et al. 2002). Longer distances are also possible. Rain-splash from leaves and soil is thought to be the main means of local spore dissemination from infected foliage in the shrub canopy to tree stems. Sporangia may also be spread by insects, although this has not been confirmed and is considered unlikely by many workers in the

US. Bark beetles, such as western oak bark beetle (*Pseudopityophthorus pubipennis*), oak ambrosia beetle (*Monarthrum scutellare*) and the minor oak ambrosia beetle (*Monarthum dentigerum*) have been investigated as potential vectors (McPherson et al. 2000). Dry wind is not thought to play an important part in the dispersal of *P. ramorum* spores since humidity and water are essential for *P. ramorum* infection to occur.

Experience from the USA has shown that stream water, as well as soil attached to hikers' boots, car tyres and to the feet of animals have been implicated in pathogen dissemination (Tjosvold et al. 2002). Davidson et al. (2005) tested hikers' footwear for *P. ramorum* in an affected Californian forest. They determined that one-third to a half of hikers had infested soil on their footwear during the rainy season. There have been similar findings in work carried out in the UK, where both streams and footwear have been confirmed as potential pathways of spread (J.F. Webber, personal communication). Streams and waterways could act as a pathway for the pathogen both within an outbreak site and possibly as a pathway for the pathogen to infect new sites. The epidemiological significance of *P. ramorum* being transmitted by waterways is yet to be fully investigated, but it would be feasible for streams to carry infectious particles, such as infected leaves and debris, over moderate distances.

An important pathway of infection in woodland is through sporulating foliar hosts such as rhododendron. In the UK, rhododendron can make up a dense woodland understorey. Rhododendron plants are often in direct contact with each other and with susceptible trees. Under favourable conditions, this might allow the tree to succumb to infection either through direct plant-to-plant contact or through the movement of spores in rain-splash. Many of these routes of dispersal are being investigated as part of the UK/EU research programmes for *P. ramorum.*

Detection and identification

Both detection and identification have been fundamental to the management of the diseases caused by *P. ramorum.*

Legislative issues

The identification of *P. ramorum* as a new *Phytophthora* species in the EU ensured that an emergency eradicatory action clause under EC plant quarantine legislation could be utilised. Quarantine legislation is primarily targeted at non-indigenous organisms that pose a new threat to a country. The legislation is triggered by official notification providing full details of the organism. The identification of the species was achieved through the use of both traditional (observation of cultural and morphological characteristics) and molecular techniques (DNA-based diagnostics) (Werres et al. 2001).

Shortly after the pathogen's role in causing both ornamental dieback (principally on *Rhododendron* species) in Europe and tree mortality in California was elucidated, work was undertaken to compare European isolates with American isolates. Geographically distinct populations and two separate ‘mating types’ (A1 and A2) were identified (see ‘Causal agent and biology’ above). The discovery of these differences led to specific framing of the emergency legislation to prevent the introduction and spread of non-European isolates on all known hosts, thus addressing the new risk of A2 mating types and North American isolates to Europe, and to prevent the movement within the EU of European isolates on its main hosts, initially on *Rhododendron* and *Viburnum* and subsequently also on *Camellia*, to prevent the spread of isolates already known in Europe on the three key hosts.

The determination of hosts is also important in the framing of phytosanitary legislation. The identification of hosts of *P. ramorum* has been achieved by:

- international sharing of information on new hosts between individual researchers and through databases such as those established by the Animal and Plant Health Inspection Service (APHIS) of the United States Department of Agriculture (USDA), the California Oak Mortality Task Force, and more recently in the EU Sixth Framework Project ‘Risks Associated with *Phytophthora ramorum*’ (RAPRA).
- laboratory tests to establish the susceptibility of ornamental, woodland shrub and heathland plant species. The results are recorded in published and regularly updated ‘Experimental host’ lists in both North America and Europe.
- inspectors alerted to look at potential new host material and being required to send in suspect samples.

The information on both natural and potential hosts has been used to develop plant health policy, including changes to basic legislation, risk management and decisions on action.

Inspection procedures and laboratory diagnosis

With specific EC quarantine legislation in place, inspection procedures were introduced for the routine examination of *P. ramorum* in plant material imported into and traded within the UK. These procedures were based on the visual inspection of symptoms. For this, regular training sessions of the PHSI were set up and photographs of symptoms on the various hosts supplied and regularly updated. The inspectors are also supplied with regularly updated lists of both experimental and naturally occurring hosts. These lists provide the PHSI with valuable information so that they can target their monitoring inspections. Growers, garden centres, supermarkets and trade organisations were also issued with a letter, poster and information sheet on the organism. In all, over 1,500 information packs were sent out. Inspection procedures were linked into sampling and testing procedures to ensure efficient and accurate diagnosis of the pathogen. The pathogen is routinely identified by isolation on selective media, followed by microscopic examination of the resulting colonies after 5–6 days. Identification can usually be made on morphological parameters alone, but a research and development programme has produced molecular assays that include both conventional and real-time polymerase chain reactions (PCR – a technique that can be used in the identification of species based on DNA sequence recognition). These assays are used to confirm an identification based on morphology. Molecular methods have also been evaluated for direct use on plant material. There has been a concerted European effort to standardise these methods with the production of a diagnostic protocol by the European and Mediterranean Plant Protection Organisation (EPPO). This provides details on symptoms, sampling and testing and includes a decision tree to ensure that sufficient tests have been completed to permit the release of test results. The use of molecular techniques has been invaluable in providing a fast, robust testing service dealing with up to 10,000 samples a year. These methods have been used alongside baiting techniques to permit soil and water testing as part of the monitoring process for the presence of *P. ramorum* in the environment and for determining the effectiveness of control measures.

More recently, at the beginning of 2005, the PHSI has also been able to utilise a new field identification kit, the lateral flow device (LFD). LFDs are immunochromatographic assays that employ similar technology to home pregnancy testing kits. They are ideal for use in the field because they are pocket-sized, produce a result within minutes, and can be used by non-specialists. The LFD currently in use has its limitations since it is only able to detect to genus level, and is somewhat user-dependent. However, LFDs have enabled the PHSI to setup an initial screening of samples, with potentially positive ones being sent to the laboratory for confirmatory diagnosis. Inspectors are also instructed to send in samples testing negative but where symptoms look very typical. This is of particular relevance for *P. ramorum* as the symptoms are indeterminate. Only about 20% of samples submitted are positive, with the vast proportion testing negative. This initial screening reduces postage and processing costs, and, more importantly, helps the PHSI to recognise *P. ramorum* symptoms in the future. These decision support tools are also supplied to other field staff who have been deployed to assist with the campaign and thus provide on-site guidance to less experienced staff.

Surveys of the wider environment

Accurate detection and identification of *P. ramorum* has been essential in surveys for the pathogen and is based on measures taken as a result of the surveys to reduce the risks associated with the disease. EU member states, including the UK, have carried out surveys of plants in the environment, in woodland sites and in established plantings such as historic gardens, parks and landscape plantings, in order to determine its presence outside nurseries. It should be noted that our awareness of the disease in nurseries relates to targeted non-random observations carried out by the PHSI for plant-passporting purposes and in follow-up investigations.

In the UK, a statistically based random survey of over 1,000 woodland sites by the forestry commission completed in April 2004 found all sites to be negative based on visual rhododendron inspection and sampling, and testing of suspect symptoms. These results indicated that *P. ramorum* primarily occurs in nursery or managed garden situations in the UK and is not widespread in the natural environment. Therefore eradication of the pathogen wherever it is found is currently considered to be an effective option.

Detection of *P. ramorum* in the natural environment is problematic and labour-intensive. The symptoms are not diagnostic and recognition requires skilled, experienced surveyors. There is a large area to survey, often with a limited staff resource, and some sites are inaccessible or difficult to survey, particularly those with large rhododendrons present. With the knowledge that *P. ramorum*, in common with *Phytophthora* species in general, has motile water-borne spores, the UK is gearing up to a further surveying exercise to include random surveying of water courses. This has been shown to be effective for environmental monitoring in the US, and also in the UK where the presence of *P. ramorum* has been detected on sites where visual plant inspections did not initially detect the disease. A baiting method used *in situ* in watercourses should provide a survey method that avoids the problems encountered in a survey based on visual detection. For the random water survey, the development of leaf baits that can be used in water has been important. Extensive experiments have been carried out to determine the best bait material (ranging from artificial baits such as agar blocks to known healthy leaves) and the best bait delivery systems (such as muslin bags attached to plastic fishing bobs). The most reliable bait (rhododendron leaves in muslin bags) has been used to determine the sensitivity of the assay in the laboratory and during a pilot study of known positive sites. Information on recovery rates from different types of watercourses and time of the year has also been gathered. This demonstrated, for example, that recovery rates were poor during the summer months (P.A. Beales, personal communication).

The use of soil baits has also been important at ongoing outbreak sites to determine where the greatest risks are, such as along pathways. Soil detection, again, relies on baiting the organism from the soil, because it is hard to detect in soil by molecular methods. Rhododendron leaves are the preferred bait, either by placing in bait bags directly into the soil or floating on flooded soil samples. These bait leaves may then be either tested by real-time PCR or by isolation.

On-site diagnosis

As detailed above, on-site diagnostic techniques have been used in the identification of the pathogen and for control of the disease and should continue to play a role. Routine use of LFDs at import inspections will allow the rapid identification of potential *P. ramorum* samples and enable prompt action by holding potentially infected consignments while laboratory tests confirm the presence or absence of the pathogen. This will be particularly important in mitigating the risk of new populations or mating types of the pathogen entering the country. The development of on-site diagnosis utilising real-time PCR technology will also be key in mitigating risks. On-site DNA extraction and real-time PCR (TaqMan®) methods have been developed that enable the diagnosis of symptomatic infections of *P. ramorum* in less than two hours (Hughes et al. 2005). They enable multiple host species and multiple samples to be screened and should play an important role in measures to control the disease. They also have the potential to detect asymptomatic infection. This technology has been used both at outbreak sites to advise on disease progression and at ports and airports to check suspect symptoms, and has the potential to monitor aysmptomatic infection in the future.

Molecular techniques versus traditional techniques

The use of molecular techniques has raised interesting questions about the significance of detection of the pathogen's DNA compared with more traditional methods based on culturing, which only detects viable propagules of the pathogen. There has been considerable debate about the value and application of each approach, depending on the end user's need. Traditional methods provide a broader screen for all *Phytophthora* species, whereas PCR methods are generally designed to be more specific. This latter approach is very helpful. But if assays are species-specific, they exclude the detection of other existing and potentially new pathogens. This means that a 'fit for purpose' approach is needed when designing testing strategies. The use of traditional isolation techniques was arguably essential for the discovery of a new *Phytophthora* species in the UK in 2003, known as *Phytophthora kernoviae* (Brasier et al. 2005b). This pathogen causes similar symptoms in several of the same host species as *P. ramorum* but has some unique characteristics (see Defra information sheet on *P. kernoviae* at www.defra.gov.uk/planth/pkernovii.htm). Through such techniques, researchers were able to detect the subtle differences in morphology between *P. ramorum* and the new species. Subsequently, molecular techniques ensured that *P. kernoviae* was promptly detected in other parts of the south-west of England close to the original finding, as well as in south Wales and a single north-west of England nursery. Comparison of sequence data from the rDNA ITS region allowed the relationship of *P. kernoviae* with other *Phytophthora* species to be determined and proved that this new species was not closely related to *P. ramorum*. The use of these DNA-based identification techniques has ensured that disease outbreaks caused by the two pathogens have been accurately identified, and disease control measures implemented accordingly.

Critical inflection points

Critical inflection points in the identification and detection process are:

- the checking of susceptible material moving in trade. For this to be effective, informed targeting of inspections from intelligence gathered on trade pathways and scientific advice on actual and potential hosts is critical, along with adequate staffing.
- the diagnosis of a suspect finding of *P. ramorum.* Rapid, accurate diagnosis ensures that there is equally rapid action to prevent spread of the pathogen. For this, adequate resources both for routine diagnosis and for further development of diagnostic methods, particularly on-site methods, will be essential.

Future

Detection and identification, alongside fundamental research into the biology of *P. ramorum*, will continue to play a role in mitigating the risks posed by the pathogen. Such reduction in risk will be achieved by ensuring that the detection of new natural and potential hosts, new symptoms, the level of host susceptibility and the potential for sporulation of existing and new hosts is reported and translated into effective risk management strategies. Advice as to which hosts require inspection, what symptoms to look for and how to control the pathogen will need to be kept up to date to prevent further spread and to reduce the socioeconomic and environmental impacts. It will also be important to continue to survey nursery and wild material to determine the distribution of *P. ramorum* and to test suspect symptoms for the pathogen. These tests should include determining the mating type (A1/A2) and population (European or North American) of the pathogen.

The use of molecular techniques through DNA profiling and sequence data will also be important in studies on the population dynamics of the pathogen and should help indicate any population differences and genetic changes as a result of the evolution of chemical resistance. Such studies may ultimately provide clues as to the origin of the pathogen.

Summary of key aspects of the pathogen

- The emergence of *P. ramorum* is thought to have been primarily driven by the international trade in plants, i.e. through pathogen pollution.
- Host–pathogen evolution is a potential driver. Genetic recombination through sexual outcrossing of A1 and A2 mating types or through somatic recombination due to fusion of zoospores of the European and North American populations may occur. This would probably increase the pathogen's adaptive fitness to a range of hosts, its virulence and its environmental fitness. This is a risk if European and North American isolates come together, or if other introductions occur from the, as yet unknown, centre of origin.
- EC phytosanitary control measures have therefore focused on keeping non-European isolates out of the EU and on preventing the spread of *P. ramorum* in the EU by attempting to ensure freedom from the pathogen in plants moving in trade.
- The origin of *P. ramorum* is unknown, but the evidence strongly suggests it is an introduced exotic pathogen. The most likely hypothesis is that it is of south-east Asian origin in ecosystems rich in either Fagaceae (e.g. *Lithocarpus*) or Ericaceae (e.g. *Rhododendron*). If *Rhododendron* is not the host on which the pathogen evolved, it is at least implicated as the principal host plant in the trade pathways for its spread. Determining the origin of the pathogen will be important to allow phytosanitary measures to be applied to plant material from that origin and to gain knowledge of host–pathogen behaviour in the pathogen's natural environment, possibly leading to new control mechanisms.

- *P. ramorum* has a wide host range. Its natural host range is continuing to expand, as is the list of experimental hosts. Some of the tree and non-tree species predicted to be susceptible by experimental work have now been found infected naturally. The continual extension of the host list makes effective legislative control difficult. Legislators must be alert to the findings of inspectors and scientists and press for appropriate modification of phytosanitary measures as speedily as possible to avoid gaps in control measures.
- The pathogen generates inoculum in the form of sporangia on the foliage of a number of non-tree hosts (e.g. rhododendron) and also some tree hosts (e.g. sweet chestnut and holm oak). It is this inoculum from foliar hosts that is likely to drive local epidemics in woodlands.
- *P. ramorum* causes damaging epidemics in the US. The likelihood of such epidemics occurring in the EU with its own particular range of ecosystems is not known but is likely to depend on climatic factors and host species composition. A need for modelling and risk mapping to predict possible epidemics has been identified and Defra has commissioned this work in the UK. There are also similar efforts elsewhere in Europe and in the US.
- There is continued concern that fungicides may be masking symptoms on plants in trade. Research on the effects that fungicides have on *P. ramorum* should provide answers.
- Wherever they are found – currently in North America and Europe – the pathogen and the diseases it causes are the subject of quarantine control. But the extent of the control varies between member states of the EU and between states in the US, depending on the extent of the pathogen in woodland and unmanaged habitats. In Europe, this is kept under review by discussion on EC measures. The 2004 surveys conducted by member states on 'uncultivated/unmanaged plants' should inform this discussion.
- Eradication action currently relies on the destruction of known or suspected infected material by burning or deep burial. The development of other forms of eradication by chemical or physical means, which would enable the removal of the infection without destroying the plant, will be welcomed by the horticultural industry. Research is under way to look at alternative methods.
- Rapid, reliable molecular detection and identification techniques are key to controlling *P. ramorum*. More routine use in the laboratory of direct PCR on plant material will facilitate more rapid screening. Further development of rapid, on-site diagnostic methods will assist this.
- Ongoing fundamental research into the biology of this newly important pathogen will continue to inform the measures that are needed to reduce the socioeconomic and environmental impacts that *P. ramorum* has or may have in the future.
- In the EU, *P. ramorum* has been subject to emergency legislation since 2002. The success of this legislation, measured by surveys in individual EU member states, will determine the eventual status of this organism in phytosanitary legislation.

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Annex

EC phytosanitary measures for the control of *Phytophthora ramorum*

In 2002, emergency EU phytosanitary legislation was adopted (Commission Decision 2002/757/EC) against the introduction into and spread within the European Community of *Phytophthora ramorum*. The legislation was amended in 2004 (Commission Decision 2004/426/EC) to take account of new information on the damage caused by *P. ramorum.*

In the overall scope of the legislation, *Phytophthora ramorum* is declared a harmful organism and the introduction into the Community and spread within the Community of both non-European and European isolates of *P. ramorum* is banned.

Specific measures for the import of plants and plant products and for Community controls on plants are laid down.

Measures are specified for the action to be taken on infected plants, inspection and treatment measures.

Import controls

- Plants susceptible to *P. ramorum** from the USA may only be introduced into the Community if they are accompanied by a phytosanitary certificate which states that they either originate in areas in which non-European isolates are known not to occur or no signs of the pathogen have been observed at their place of production during official inspection.
- Wood of species susceptible to *P. ramorum** may only be introduced into the Community from the USA if it originates in areas where the pathogen is known not to occur. It also has to be stripped of bark and either squared to remove the rounded surface or have not more than 20% water content or be disinfected by an appropriate hot-water treatment. An alternative to the measures outlined in the last sentence is that wood, with or without bark, be identified as kiln-dried to below 20% moisture content.
- Plants of *Viburnum* species, *Camellia* species and *Rhododendron* species (excluding *R. simsii*), other than fruit and seed, from third countries other than the USA can only be moved within the Community if accompanied by a plant passport.
- Bark from susceptible trees growing in the USA is not to be permitted entry into the Community.

* Susceptible species currently specified in the regulations are *Acer macrophyllum*, *Aesculus californica*, *Arbutus menziesii*, *Arctostaphylos* spp., *Heteromeles arbutifolia*, *Lithocarpus densiflorus*, *Lonicera hispidula*, *Quercus* spp., *Phamnus californica*, *Rhododendron* spp. (other than *R. simsii*), *Umbellularia californica*, *Vaccinium ovatum* and *Viburnum.*

Community controls

- Plants of *Rhododendron*, other than *R. simsii*, *Camellia* spp. and *Viburnum*, other than fruit and seed, originating and moving within the Community must be accompanied by a plant passport.
- The plant passport requires that either:
  - the material originates in areas in which *P. ramorum* is known not to occur

  or

  - the plants have been subject to official inspections and there have been no signs of *P. ramorum* on the plants at the place of production.
- If *P. ramorum* is found, an appropriate eradication programme must be implemented before any trading of plants can continue. A minimum set of eradication measures has been laid down whereby all infected plants and susceptible plants within a 2m radius of the infected plants must be destroyed along with any associated growing media. All susceptible plants grown within a 10m radius of the infected plants must be held *in situ* for at least three months of active growth and subjected to at least two additional inspections. No pesticide treatments that may suppress symptoms of *P. ramorum* can be used on any susceptible plants within a 10m radius of an infected host or any plants remaining from an affected lot for three months after eradication has been undertaken. Finally, all other susceptible material at the place of production must also have been subject to an official intensive re-inspection during this period.
- Member states of the Community have also been obliged to conduct official surveys for the pathogen and provide results to the Commission and other member states. The surveys must include both 'cultivated and uncultivated/unmanaged plants'.
- When signs of *P. ramorum* are found on plants other than on places of production, member states have to 'take appropriate measures to at least contain' *P. ramorum*.

The EC legislation is implemented in the UK by the Plant Health (*Phytophthora ramorum*) (England) Order 2004 No. 2590, the Plant Health (*Phytophthora ramorum*) (Scotland) Order 2002 No. 223 and the Plant Health (Wales) (*Phytophthora ramorum*) (Wales) Order 2002 No. 1350 (W.130) Also, the Plant Health (Forestry) (*Phytophthora ramorum*) (Great Britain) Order 2002 No. 2589, the Plant Health (*Phytophthora ramorum*) (Northern Ireland) Order 2003 No. 193 and the Plant Health (Wood and Bark) (*Phytophthora ramorum*) (Northern Ireland) Order 2003.

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