

Status of *Phytophthora ramorum* and *P. kernoviae* in Europe¹

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Abstract

Following the recognition that *Phytophthora ramorum* (the cause of sudden oak death in the U.S.) was present in Europe as well as America, emergency European Community (EC) phytosanitary measures were put in place in September 2002 to prevent spread of *P. ramorum*, and also to stop introductions of the pathogen from elsewhere. A 3 year European project then started in 2004 to assess the risks posed by *P. ramorum* to trees and environmentally important habitats in Europe. The project – ‘Risk Analysis of *Phytophthora ramorum*’, known by the acronym RAPRA, involves eight research organizations in six countries. The aim is to develop a European pest risk analysis (PRA) for American and European populations of *P. ramorum*. A project objective is to disseminate results through outreach activities, formal presentations and the project website (<http://rapra.csl.gov.uk>). The website hosts an extensive database which has gathered together all the records of plants infected by *P. ramorum* in EU member states, as well as information on host susceptibility and differences between American and European populations of the pathogen.

During surveys to establish the extent of *P. ramorum* in the U.K., another new species of *Phytophthora* was discovered and has since been named *Phytophthora kernoviae*. Like *P. ramorum*, *P. kernoviae* is a serious foliar pathogen on rhododendron and also causes bleeding stem lesions on European beech (*Fagus sylvatica*). The current distribution of these two pathogens is described as well as the number of trees affected in Europe. In addition, some of the most recent research findings that have emerged from the RAPRA project are discussed including data on pathogen biology, breeding system and disease epidemiology, and compared with our growing understanding of the behavior of *P. kernoviae*.

Key words: *Phytophthora kernoviae*, *P. ramorum*, sudden oak death, rhododendron, bleeding canker, European ecosystems.

Introduction

Phytophthora ramorum (the cause of sudden oak death in California and Oregon) is acknowledged as a potential threat to European trees, woodland ecosystems and other environmentally important habitats. Only formally described and named in 2001 (Werres and others 2001), *P. ramorum* is recognized as a recent alien introduction to both the U.S. and Europe³. It is currently considered to be one of the most significant quarantine pathogens for Europe. Prior to being named, the pathogen was first

¹ A version of this paper was presented at the Sudden Oak Death Third Science Symposium, March 5–9, 2007, Santa Rosa, California.

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³ Commission decision of 19 September 2002 to prevent the introduction into and spread within the Community of *Phytophthora ramorum* Werres, De Cock & Man in't Veld sp. nov. (notified under document number C–2002 3380).

observed infecting foliage of rhododendron in Germany in 1993, but its relevance as the cause of sudden oak death (SOD) in the U.S. was not understood until 2001. However, the potential risk that SOD poses to Europe resulted in the European Commission decision of 19 September 2002. This put measures in place to stop further introductions of *P. ramorum* and prevent it spreading within Member States (MS). It included the requirement for all MS to carry out annual surveys of nurseries (and a year later also to survey the natural environment), to establish the status of *P. ramorum* in each country. In addition the European Commission funded the 3 year research project - Risk Analysis of *Phytophthora ramorum* (acronym RAPRA, FP6 Project 502672) to generate information about *P. ramorum* that was relevant to Europe and could inform changes to EU policy related to the pathogen.

***Phytophthora ramorum* in Europe**

Since finding *P. ramorum* in southern England in 2002 (Lane and others 2003), the U.K. has reported around 580 outbreaks in nurseries/plant retail outlets, with more in gardens, parks and woodlands (<http://www.defra.gov.uk/planth/pramorur.htm>). Elsewhere in Europe *P. ramorum* has been found in nurseries and formally reported from 15 other countries: Belgium, Czech Republic, Denmark, Finland, France, Germany, Ireland, Italy, the Netherlands, Norway, Poland, Slovenia, Spain, Sweden, Switzerland, (although it is now considered as eradicated from the Czech Republic). As with the U.K., hosts of *P. ramorum* have mainly been ornamental plants from the genera *Rhododendron*, *Viburnum*, *Camellia* and *Pieris*.

The findings of *P. ramorum* outside nurseries have included public and privately owned green areas as well as woodlands. In the U.K. (mainly England and Wales with just two outbreaks in Scotland) the disease has been confirmed at around 160 locations (<http://www.defra.gov.uk/planth/pramorur.htm>). Elsewhere in Europe (the Netherlands, Germany, Ireland, Norway, Slovenia and Switzerland) the number of findings of *P. ramorum* from outdoor locations varies widely but is generally much lower than the U.K., and the majority of infestations have been on rhododendron (see RAPRA website for more information: <http://rapra.csl.gov.uk>). In just two of these countries (England and the Netherlands), *P. ramorum* has also been found causing bleeding stem lesions on a range of tree species (table 1 and Brasier and others 2004).

In addition, it has become apparent in the infestations that occur beyond the confines of nurseries, both ornamental shrubs and some tree species can suffer from leaf and shoot infections. In the U.K. the evergreen oak, *Quercus ilex*, has been the most frequently found tree with *P. ramorum* leaf and shoot infections. However, other woodland species such as *Castanea sativa*, *Fraxinus excelsior* and *Q. cerris* as well as ornamental species of *Drimys*, *Magnolia*, *Michelia*, *Cinnamomum* and even *Eucalyptus* have been found with foliar infections (see <http://rapra.csl.gov.uk>). When this occurs, the disease has usually become well established on rhododendron prior to

Table 1—Trees with *P. ramorum* infected stem (bole) cankers in Europe.

Country	Tree Species*	Family	Number
England	<i>Aesculus hippocastanum</i>	Hippocastanaeae	1
England	<i>Acer pseudoplatanus</i>	Aceraceae	1
England	<i>Castanea sativa</i>	Fagaceae	1
England	<i>Fagus sylvatica</i>	Fagaceae	6
Netherlands	<i>Fagus sylvatica</i>	Fagaceae	6
England	<i>Nothofagus obliqua</i>	Fagaceae	2
England	<i>Quercus acuta</i>	Fagaceae	1
England	<i>Quercus cerris</i>	Fagaceae	5
England	<i>Quercus falcata</i>	Fagaceae	1
England	<i>Quercus petraea</i>	Fagaceae	1
Netherlands	<i>Quercus rubra</i>	Fagaceae	8
England	<i>Schima</i> sp.	Theaceae	1
Total			34

* Data from RAPRA database on naturally infected hosts, <http://rapra.csl.gov.uk>

foliage of trees becoming infected. Thus it is uncertain whether foliar infection of a European tree such as *Q. ilex* could sustain a *P. ramorum* epidemic in the same way that tanoak or bay laurel do in the U.S. Nonetheless, it remains a possibility and highlights the risk that this pathogen could pose to the Mediterranean holm oak forests of southern Europe (Moralejo and others 2006).

Factors Affecting *P. ramorum* Disease in Europe

In the U.K., *P. ramorum* has been found most often in planted woodland-gardens which host a wide range of non-native and exotic plants, but particularly where species and cultivars of rhododendron dominate. Where it is found infecting trees in woodlands, invariably a key understorey component is *Rhododendron ponticum*, an invasive species in its own right, which has become naturalized in many areas with acidic soils. Laboratory tests have shown that not only is rhododendron generally highly susceptible to infection by *P. ramorum*, but it can also support abundant sporulation (Denman and others 2006a, b; Morelajo and others 2007). There is no doubt that this host has played a key role in disease escape into the natural and semi-natural environments and the subsequent spread to trees. It is also the most frequently infected host in non-nursery outbreaks in other European countries.

However, in ecosystems in Europe where rhododendron is less abundant or absent, other plant species may take on the equivalent role and support abundant sporulation by *P. ramorum*. Some of the most important ecosystems at risk probably include the holm oak forest and laurisilva ('laurel forest') of southern Europe. These are home to several other tree and understorey species such as *Q. ilex*, *Rhamnus alaternus*, *Viburnum tinus*, and *Arbutus unedo*, all of which have the potential to support moderate to high levels of sporulation (Morelajo and others 2006). Species of *Vaccinium* have also been shown to be capable of supporting levels of sporulation

similar to those observed on Californian bay laurel and therefore could potentially sustain the disease in heathland habitats (Defra Report 2005).

Apart from the combination of trees with susceptible stems growing close to foliar hosts infected by *P. ramorum* and able to support abundant sporulation, climate plays a crucial role in disease establishment and development. To determine which parts of Europe could be at greatest risk based on climate alone, comparisons were made in 2003 using a climate matching model (CLIMEX) to compare southern Oregon, where *P. ramorum* is present, with Europe (R. Baker, Central Science Laboratory; member of the RAPRA Consortium). The comparison was then revised based on Meentemeyer and others (2004) and this identified the west of the U.K., Ireland and northwest parts of France, Spain and Portugal as regions with the closest eco-climate matching in relation to *P. ramorum*. Since then, the findings of *P. ramorum* outside nurseries have been most common in southwestern parts of England and Wales, where the combination of abundant understorey rhododendron and mild, often wet climate, appears to have provided a near perfect environment for the pathogen.

Another Aerial *Phytophthora*, *P. kernoviae*

Following the initial findings of *P. ramorum* in nurseries in the U.K., there have been a number of surveys; initially to determine how widely it was present and later to monitor spread. Identification of the areas most likely to harbour *P. ramorum*, based on climatic and host criteria, meant that particular emphasis was placed on surveying woodlands and woodland-gardens in the southwest of England. These revealed that a number of sites in Cornwall had *R. ponticum* and other *Rhododendron* cultivars heavily infected with *P. ramorum*, but also found another new and invasive *Phytophthora* species now named *P. kernoviae* (Brasier and others 2005). In much the same way as *P. ramorum*, *P. kernoviae* appeared to be a serious foliar pathogen on rhododendron and caused bleeding lesions on European beech (*Fagus sylvatica*).

Since the discovery of this new pathogen in November 2003 (Brasier and others 2004), *P. kernoviae* has been found extensively in an area of about 14.24 square km (5.5 square miles) in southern Cornwall between Redruth and Falmouth which is now defined as the *Phytophthora kernoviae* Management Zone or PkMZ (Anonymous 2004). It has been reported from one nursery in Cornwall, and also found at several other sites (mainly woodland) outside the PkMZ but still in the same county. There has also been a small cluster of outbreaks in Wales near Swansea, with a possible link between this cluster and one of the outbreak sites in the PkMZ. The only other occurrences of *P. kernoviae* in the U.K. have been limited to a single mature infected rhododendron in a managed garden and an outbreak in a nursery, both in the north of England and both now eradicated (Sansford 2007). Although *P. kernoviae* is considered to be one of several invasive tree *Phytophthoras* recently arrived in the U.K. (Brasier and others 2005), its origin is unknown and until recently it had not been reported from elsewhere. However, in March 2006 the New Zealand Ministry of Agriculture and Forestry announced findings of *P. kernoviae* in two separate localities on the North Island in New Zealand. At one of the sites it had caused necrosis on the shoots and fruits of cherimoya (*Annona cherimola*), and at the other site in the Trounson Kauri Park it had been isolated from soil. The status of *P. kernoviae* in New Zealand, either as a native or introduced species, has yet to be clarified.

Various aspects of the biology and epidemiology of both *P. ramorum* and *P. kernoviae* have been studied and compared. Both are aerial *Phytophthoras* which infect and sporulate abundantly on rhododendron, and both produce caducous sporangia. The two species apparently thrive under the same climatic conditions and can cause lethal bleeding cankers on mature trees and even overlap at the same site. This can lead to very intimate contact between the pathogens, and they have been found infecting the same rhododendron plant and even both causing separate bleeding cankers on the same tree (Brown and others 2006).

So far the range of tree species that *P. kernoviae* has been found infecting is much smaller than has been recorded for *P. ramorum*. The majority of trees with cankers caused by *P. kernoviae* consist of beech (around 55 in total), with two oaks (*Q. robur*) and one *Liriodendron tulipifera* infected. Lesion extension has been found to be very rapid in some trees, and can result in tree mortality in just a few years. As with *P. ramorum*, *P. kernoviae* infects the foliage of some ornamental shrubs (Beales and others 2006) but the host range is much smaller (primarily *Rhododendron* and *Pieris*). Some tree species have also been found with infected foliage; this includes a wide range of *Magnolia* species (Denman and others 2005), *Q. ilex*, *Michelia doltsopa* and *Drimys winterii* (S. Denman, unpublished data). There are also several critical differences between the two *Phytophthoras*. Not least, the two pathogens have different breeding systems: *P. ramorum* is heterothallic (Werres and others 2001) whereas *P. kernoviae* is homothallic (Brasier and others 2005). To date *P. kernoviae* has only been found in two nurseries in England, whereas *P. ramorum* has been found in close to 600 nurseries and garden centers throughout the U.K.

New Research Findings

Research has now been underway on the biology and epidemiology of both these *Phytophthora* pathogens for at least 4 years in Europe via RAPRA and other projects. The findings feed into the PRAs that are being undertaken to assess the risk that these pathogens pose to the U.K. and elsewhere in Europe. The outcome of work testing susceptibility to *P. ramorum* on more than 260 species and reports of 140 naturally infected host species in Europe are given in two large databases on the RAPRA website (<http://rapra.csl.gov.uk>). Even though susceptibility tests often introduce inoculum via wounds, it has been shown that zoospores of *P. ramorum* can penetrate mature, intact bark of tree species such as beech (*F. sylvatica*), sweet chestnut (*C. sativa*) and Douglas fir (*Pseudotsugae menziesii*) leading to infection (Brasier and Kirk unpublished). *Phytophthora ramorum* and *P. kernoviae* have also been recovered from discolored xylem 5 to 25 mm below exposed sapwood surfaces of naturally infected trees more than two years after the overlying bark was removed. Both pathogens probably commonly occupy xylem beneath phloem lesions and persist and even grow in that tissue (Brown and Brasier 2007). There is also evidence of the development of fungicide resistance in *P. ramorum*. In one study, around 25 percent of a sample of 71 *P. ramorum* isolates obtained mainly from infected nursery plants from various European countries showed resistance to the chemical metalaxyl-M (Wagner and others 2004).

Understanding the breeding system of *P. ramorum* and the potential for interbreeding between European and American lineages of *P. ramorum* (Ivors and others 2006) remains central to assessing the risk this pathogen poses to Europe and indeed other parts of the world. As a heterothallic species, both A1 and A2 mating types are required for sexual recombination in *P. ramorum* and the European lineage is

predominantly A1 whilst in the U.S. it is A2. Extensive testing of isolates from Europe and America as part of the RAPRA project has confirmed this separation between continents of the mating types with two exceptions (Werres and others 2007). These are 1) findings of A1 European lineage in nurseries in Oregon and Washington state (Hansen and others 2003) and 2) the discovery of at least three isolates in Belgium which appear to be of European lineage but of A2 mating type (minutes of the EU Plant Health Standing Committee meeting on 26–27 November 2006). Moreover, in studies which looked at the success of mating between A1 and A2 isolates of *P. ramorum*, a surprisingly high frequency (average about 57 percent) of gametangia were abnormally developed or contained visibly aborted oospores; an even higher proportion were classified as non-viable following vital staining (Brasier and others 2007). Despite this, although the frequency of viable, mature oospores in *P. ramorum* is comparatively low (compared with other *Phytophthora* species), there is clearly potential for genetic recombination of *P. ramorum* via the sexual stage.

However, probably some of the most striking, recent findings about both *P. ramorum* and *P. kernoviae* relate to the discovery of asymptomatic aerial infection following exposure in the field to these pathogens. Furthermore, there is evidence of sporulation from some of these asymptomatic leaves and fruits (Denman and others 2007). Infected but symptom free roots may also harbour *P. ramorum*. Following exposure to zoospores and a period of incubation, potted *Rhododendron* plants were examined using microscopy and revealed there were *P. ramorum* chlamydospores visible in the roots but no evidence of necrosis (Reidel and others 2007). Both findings have clear implications for the control of disease spread by these pathogens, particularly for the nursery trade.

Literature Cited

Anonymous. 2004. The Plant Health (*Phytophthora kernoviae* Management Zone) (England) Order 2004. The Stationery Office, ISBN0110513878.

Beales, P.A.; Lane, C.R.; Barton, V.C.; Giltrap, P.M. 2006. *Phytophthora kernoviae* on ornamentals in the U.K. EPPO Bulletin 36: 377–379.

Brasier, C.; Denman, S.; Brown, A.; Webber, J. 2004. Sudden oak death (*Phytophthora ramorum*) discovered on trees in Europe. Mycological Research. 108: 1108–1110.

Brasier, C.M.; Beales, P.A.; Kirk, S.A.; Denman, S.; Rose, J. 2005. *Phytophthora kernoviae* sp. nov., an invasive pathogen causing bleeding stem lesions on forest trees and foliar necrosis of ornamentals in the U.K. Mycological Research. 109: 853–859.

Brasier, C.M.; Kirk, S.A.; Webber, J.F. 2007. Probability of sexual recombination between European A1 and American A2 isolates. RAPRA Deliverable Report: <http://rapra.esl.gov.uk>

Brown, A.; Brasier, C.; Denman, S.; Rose, J.; Kirk, S.; Webber, J. 2006. Tree hosts as aerial *Phytophthora* infections with particular reference to *P. ramorum* and *P. kernoviae* at two U.K. survey sites. In: Progress in Research on *Phytophthora* Diseases of Forest Trees. Brasier C.M., Jung T., Oßwald W. (eds). Proceedings of the 3rd International IUFRO Working Party 7.02.09 Meeting, Freising, Germany. 11th–17th September 2004. Forest Research, Farnham, U.K.: 166–173.

Brown, A.V.; Brasier, C.M. 2007. Colonization of tree xylem by *Phytophthora ramorum*, *P. kernoviae* and other *Phytophthora* species. Plant Pathology. 56: 227–241.

Defra Report. 2005. *Phytophthora ramorum* epidemiology: sporulation potential, dispersal, infection, latency and survival. Project PH0194.
http://www.defra.gov.uk/science/project_data/DocumentLibrary/PH0194/PH0194_2004_FRP.pdf

Denman, S.; Kirk, S.; Whybrow, A.; Webber, J. 2005. Magnolias diseased by *Phytophthora kernoviae*: Their fate in the balance?
http://archives.eppo.org/MEETINGS/2005_meetings/ramorum_presentations/Denman.doc

Denman, S.; Orton, E.; Kirk, S.; Brasier, C. 2006a. Sporulation potential of *Phytophthora ramorum* on detached leaves of some susceptible U.K. trees *in vitro*. In: Progress in Research on *Phytophthora* Diseases of Forest Trees. Brasier C.M., Jung T., Oßwald W. (eds). Proceedings of the 3rd International IUFRO Working Party 7.02.09 Meeting, Freising, Germany 11th–17th September 2004. Forest Research, Farnham, U.K.: 75-78.

Denman, S.; Whybrow, A.; Orton, E.; Webber, J.F. 2006b. *Phytophthora kernoviae* and *P. ramorum*: host susceptibility and sporulation potential on foliage of susceptible trees. EPPO Bulletin 36: 373–376.

Denman, S.; Kirk, S.A.; Webber, J.F.; Moralejo, E. 2007. Sporulation of *Phytophthora ramorum* and *P. kernoviae* on asymptomatic foliage. This volume.

Hansen, E.M.; Reeser, P.W.; Sutton, W.; Winton, L.; Osterbauer, N. 2003. First report of A1 mating type of *Phytophthora ramorum* in North America. Plant Disease. 87: 1267.

Ivors, K.; Garbelotto, M.; De Vries, I.; Ruyter-Spira, C.; Te Hekkert, B.; Rosenweig, N.; Bonants, P. 2006. Microsatellite markers identify three lineages of *Phytophthora ramorum* in US nurseries, yet single lineages in US Forest and European nursery populations. Molecular Ecology. 15: 1493–1505.

Lane C.R.; Beales, P.A.; Hughes, K.J.D.; Griffin, R.L.; Munro, D.; Brasier, C.M.; Webber, J.F. 2003. First outbreak of *Phytophthora ramorum* in England on *Viburnum tinus*. Plant Pathology. 52: 414.

Meentemeyer, R.; Rizzo, D.; Mark, W.; Lotz, E. 2004. Mapping the risk of establishment and spread of sudden oak death in California. Forest Ecology and Management. 200: 195–214.

Morelejo, E.; Puig, M.; Garcia, J.; Descals, E. 2006. In vitro susceptibility of leaves and fruits of Mediterranean shrubs to *Phytophthora ramorum*. In: Progress in Research on *Phytophthora* Diseases of Forest Trees. Brasier C.M., Jung T., Oßwald W. (eds). Proceedings of the 3rd International IUFRO Working Party 7.02.09 Meeting, Freising, Germany 11th–17th September 2004. Forest Research, Farnham, U.K.: 166–173. 69–74.

Morelajo, E.; Denman, S.; Beales, P.; Webber, J. 2007. The ability of key tree and non-tree hosts to support inoculum production of *P. ramorum*. RAPRA Deliverable Report 27: <http://rapra.csl.gov.uk>

Reidel, M.; Wagner, S.; Goetz, M.; Werres, S. 2007. Studies on the tissue colonization in *Rhododendron* by *Phytophthora ramorum*. Proceedings of the sudden oak death third science symposium. This volume.

Sansford, C. 2007. Revised summary pest risk analysis for *Phytophthora kernoviae* previously informally known as *Phytophthora* Taxon C. <http://www.defra.gov.uk/plant/pra/forest.pdf>

Werres, S.; Marwitz, R.; Man In 'T Veld, W.A.; De Cock, A.W.A.M.; Bonants, P.J.M.; De Weerd, M.; Themann, K.; Ilieva, E.; Baayen, R.P. 2001. *Phytophthora ramorum* sp. nov., a new pathogen on *Rhododendron* and *Viburnum*. Mycological Research. 105: 1166–1175.

Wagner, S.; Kaminski, K.; Werres, S. 2004: Comparative susceptibility of European and US isolates of *P. ramorum* to antifungal agents. USDA Report 03-JV-11272138-300.

Werres, S.; Kaminski, K.; Bonants, P.; Brasier, C. 2007 Relative frequency of A1 and A2 mating types in European and American populations of *P. ramorum*. RAPRA Deliverable Report 10. <http://rapra.csl.gov.uk>