DATASHEET FOR *PHYTOPHTHORA RAMORUM*

This Datasheet replaces the 15 October 2003 Pest Risk Analysis for *Phytophthora ramorum*. Further consideration of the risks to the UK will be undertaken in the new Pest Risk Analysis for the EU, which will be derived from the information presented in this new Datasheet and the findings of the EU research project RAPRA.

PREAMBLE

This Datasheet accounts for the key facts related to the plant pathogen *Phytophthora ramorum*. It has been prepared for the purpose of a policy review for the UK in 2007/08. It is not a full literature review but it does account for the results of the UK research programme as well as key aspects of the European and US research programme. It does not account for the recent reports from the IUFRO meeting, '*Phytophthoras* in Forests and Natural Ecosystems' Monterey, August 2007 which are pending publication. It has been reviewed by UK researchers and recently, by the US Forest Service, whose comments have been accounted for.

PATHOGEN IDENTITY

Name: *Phytophthora ramorum* S. Werres, A.W.A.M. de Cock & W.A. Man in 't Veld
Synonyms: None
Taxonomic position: Stramenopila; Oomycetes; Peronosporales; *Phytophthora*
Common names of the disease: Ramorum bleeding canker (sudden oak death in the USA), ramorum dieback, ramorum blight (Hansen *et al*., 2002).

Special notes on taxonomy or nomenclature: DNA sequence analysis and morphological characteristics show that *P. ramorum* is distinct from the other species of *Phytophthora* known worldwide (estimated to be over 100 different species). Based on DNA sequence data, *P. ramorum* is most closely related to *P. lateralis* and *P. hibernalis* (Garbelotto *et al.,* 2001; Martin and Tooley, 2003; Ivors *et al*., 2004). *Phytophthora ramorum* is placed into the traditional *Phytophthora* morphological Group IV of Waterhouse (1963) (and see Stamps *et al*., 1990; Erwin and Ribeiro, 1996).

Phytophthora ramorum is known to exist as two mating types, A1 and A2. Initially, European isolates were found to belong to the A1 mating type, whilst North American isolates were A2. Differences in aggressiveness, growth rate and colony type (Defra, 2005a; Brasier *et al.,* 2002; Brasier, 2003) as well as subtle differences in the sporangial morphology of the two groups of isolates (Zielke and Werres, 2002) have been observed between European and North

American isolates. DNA profiling studies, such as amplified fragment length polymorphism (AFLP) analysis (Ivors *et al*., 2004) has provided good evidence that the European and North American isolates represent distinct populations, but not distinct species, of *P. ramorum*.

In 2003, a single A2 mating type of the European population was found in Belgium (Werres and De Merlier, 2003). Since that finding, two further A2 isolates of the European population have been found there. In North America, isolates of the A1 mating type of the European population have been found on ornamental hosts in nurseries in northern Oregon, Washington and British Colombia, Canada (Hansen *et al*., 2003; Osterbauer *et al*., 2004).

A recent study using micro-satellite markers has now confirmed three known lineages (Ivors *et al*., 2006). These are what have previously been termed as a 'European population' (now referred to as the EU1 lineage) and a 'North American population' (NA1 lineage), along with a new, third lineage proposed in their study (the NA2 lineage). The EU1 lineage is predominantly A1, except for the three A2 isolates from Belgium nurseries, and has been detected in Europe and some North American nurseries. The NA1 lineage consists of A2 isolates and is present in Californian and Oregon forests and has also been detected in North American nurseries. The new NA2 lineage consists of A2 isolates, which were found in, or could be traced back to, nurseries in Washington State and California, USA. Several different genotypes were found amongst isolates belonging to this lineage leading the authors to suggest that this lineage may have a significant presence in US nurseries. The lineages are summarised in Table 1.

Table 1. Characteristics of the three lineages of *Phytophthora ramorum* (updated from Ivors *et al*., 2006 to account for the additional Belgium A2 isolates).

Lineage	Provenance	Microsatellite profile	Mitochondrial *coxI* sequence	Growth rate[1]	Colony type[2]	Mating type
EU1	EU and US nurseries	Clade 1	Unique (EU)	Fast	Aerial	A1*
NA1	US forests and nurseries	Clade 2	Unique (US)	Slow	Appressed	A2
NA2	US nurseries	Clade 3	Unique (WA)	Fast	Aerial	A2

*Includes three A2 isolates from Belgium nurseries
[1]Growth rate determined on V8 agar
[2]Mycelial growth habit on V8 agar at room temperature

EPPO listing: Alert List.
EC Annex designation: Subject to emergency EC legislation from 1 November 2002 (Anon., 2002, Anon., 2004; Anon., 2007a).

HOSTS

Phytophthora ramorum has a wide natural host range. At present, species in over 70 different genera representing 33 different families of plants have been recorded as natural hosts. A full list of natural hosts, together with geographical details and family is given in Appendix 1.

As of October 2007, *P. ramorum* has been found to cause foliar infections on 69 individual trees at 15 sites and stem cankers on 22 trees at 8 sites (J. Webber, *personal communication*). UK tree species infected include leaf infection on *Quercus ilex* (holm oak), *Quercus cerris* (Turkey oak), *Castanea sativa* (sweet chestnut), *Castanopsis orthocantha* (castanopsis), *Cinnamomum camphora* (camphor tree), *Fraxinus excelsior* (ash), *Michelia doltsopa*, *Drymis winterii* (winter's bark), *Acer laevigatum* (evergreen maple), *Cornus kousa* x *capitata*, an unconfirmed species of *Eucalyptus*, *Osmanthus delavayi* (Delavay osmanthus) and *Schima wallichii* (Chinese guger tree) as well as several species of *Magnolia*. Bleeding cankers have been observed on *Fagus sylvatica* (beech) as well as several species of *Quercus* (*Q. cerris*, *Q. petraea*, *Q. falcata*, *Q. acuta*), *Aesculus hippocastanum* (horse chestnut), *Nothofagus obliqua* (roble beech), *Castanea sativa* (sweet chestnut), *Acer pseudoplatanus* (sycamore) and a species of *Schima* (possibly *S. yunnanensis* but yet to be confirmed). Most bleeding canker infections on trees have been linked with infected *Rhododendron* plants, some infections appear to be associated with water run-off from branch forks, whilst others are only explained by inoculum dispersal distances of over 50m (Brasier and Jung, 2006). Outbreaks on nurseries make up the majority of outbreaks of *P. ramorum* in the UK. In England and Wales, 96% of nursery findings have been made on *Rhododendron*, *Viburnum* and *Camellia* – the three genera that are subject to the Plant Passporting regime for *P. ramorum* in the EU (Slawson *et al*., 2007).

The Netherlands is the only other European country where established trees have also been affected; infections on *Quercus rubra* (northern red oak) and *F. sylvatica* (beech) have been reported. These trees were all found near infected *Rhododendron* plants. In nurseries, infected *Rhododendron*, *Viburnum* and *Taxus* x *media* have been reported.

In other European countries where the pathogen has been observed outdoors, *Rhododendron* and *Viburnum* are the main hosts affected, although individual outdoor infections have also been observed on *Pieris* and *Photinia*. A wide range of ornamental plants has been affected in nursery environments in Europe. A wide range of hosts has also been reported for nurseries in Canada.

In the USA, symptoms of tree death were first observed on tanoak (*Lithocarpus densiflorus*). Substantial mortality has been observed in tanoak trees and several oak tree species including coast live oak (*Quercus agrifolia)*, Californian black oak (*Quercus kelloggii)* and shreve oak (*Quercus parvula* var. *shrevei)* as well as twig and foliar diseases in numerous other plant species, particularly on California bay laurel (*Umbellularia californica)* which is

an epidemiologically significant host. Twigs of Douglas fir (*Pseudotsuga menziesii*) along with the regrowth/young saplings and foliage of coast redwood (*Sequoia sempervirens*) have also been recorded as infected. Affected nursery hosts in the USA include species of *Pieris, Rhododendron, Viburnum, Magnolia, Osmanthus* and *Camellia* along with isolated reports of *Nerium oleander* (oleander), *Euonymus kiautschovicus* (spreading euonymus), *Arctostaphylos uva-ursi* (bearberry) and *Prunus laurocerasus* (cherry laurel) and others.

The results of experimental host testing are listed in Appendix 2. Over 110 different plant genera contain at least one species that is susceptible to the pathogen in laboratory tests. Forty-six of these genera have plants that were determined to be highly susceptible to the pathogen in at least one experiment. Many of these genera already have species that have been recorded as natural hosts. *Buddleja, Ceratonia, Cercis, Clematis, Gleditsia, Laburnum, Lantana, Larix, Olea, Oxydendrum, Pinus, Pistacia, Ribes, Sambucus* and *Tsuga* are genera which all have at least one highly susceptible species by experiment but for which there has been no recording of natural hosts in that genera to date.

Experimental susceptibility of tree species

The results of susceptibility testing of tree species are embedded in Appendix 2 along with the non-tree hosts. However, the key findings are described in more detail below. Reports are available from the Forestry Commission website: http://www.forestry.gov.uk/forestry/KIRN-5LDLRQ

Based on log tests involving wounded bark of logs from mature trees, species could be grouped into the following susceptibility categories: 'more' susceptible; 'less' susceptible; resistant:

For *P. ramorum*, 'more' susceptible species included: *F. sylvatica* (beech), *Q. cerris* (Turkey oak), several American red oak species (including *Quercus rubra*), *A. pseudoplatanus* (sycamore), several *Nothofagus* species (southern beeches), *C. sativa* (sweet chestnut), *P. menzeisii* (Douglas fir), *Tsuga heterophylla* (western hemlock) and some firs (*Abies* spp.); common oak (*Quercus robur*) and sessile oak (*Q. petraea*) were less susceptible.

Results from *P. ramorum* log tests with unwounded bark are reported in Defra, 2005c. Infection could occur without wounding on *F. sylvatica, Q. robur, Q. rubra, C. sativa, P. sitchensis* (sitka spruce), and *P. menziesii* (Douglas fir).

Results from testing saplings is also reported in Defra 2005c. In general, results supported the host susceptibilities found in log tests, with only a few exceptions. Saplings were only infected by *P. ramorum* when wounded; susceptibility varied with season. Beech and sweet chestnut were consistently highly susceptible to *P. ramorum* in wound-inoculation tests. Stems of magnolia had low susceptibility.

GEOGRAPHICAL DISTRIBUTION

North America: The pathogen has been reported in the wild in parts of California and Oregon. Infected material has been found in nurseries in more than 20 other states. The pathogen has also been reported in nurseries and in residential gardens in British Columbia, Canada (Anon., 2006a).

Symptoms of tree death were first observed on tanoak (*L. densiflorus*) in California in 1995. The cause of death was unknown at the time but since then, substantial tree mortality has been observed in tanoak (*L. densiflorus*) and several oak species. In July 2001, the pathogen was also found in Oregon forests. The pathogen was identified in nursery stock in California in 2001, but the North American nursery industry was not widely affected until 2003 when the pathogen was detected in California, Oregon, Washington, and British Columbia (Canada) nurseries (COMTF, undated).

The pathogen is currently present in forest environments in the Californian counties of Marin, Santa Cruz, Sonoma, Napa, San Mateo, Monterey, Santa Clara, Mendocino, Solano, Alameda, Contra Costa, Humboldt, Lake, and San Francisco as well as in Curry County, Oregon. Presently, the pathogen is subject to eradication and containment measures where found on nurseries, although eradication is no longer considered feasible at wild sites in California. Attempts to eradicate the pathogen in forests in Curry County, Oregon have been undertaken since its discovery there. The distribution of the pathogen in Oregon appears to be limited to a small area near the town of Brookings suggesting that the eradication effort there has at least slowed the progress of the pathogen (Kanaskie *et al*., 2007). Ongoing surveys of nurseries and regulation of nursery stock continue to limit the pathogen's spread.

In Canada, *P. ramorum* was first detected in June 2003 on four rhododendron plants at one nursery in British Columbia and one rhododendron plant on a residential planting originating from the infested nursery. National surveys of nurseries, public parks and gardens and forested areas that year and the previous year did not detect the pathogen (Anon., 2006a). However, in 2004 a Californian nursery had shipped camellia plants to Canada that were later found to have tested positive for *P. ramorum*. Subsequent investigations detected the pathogen in Californian material at nine retail garden centres in British Columbia. Further survey and trace back/trace forward activities revealed the presence of the pathogen at 35 sites in British Columbia. Ten of these sites were residential gardens with camellia plants associated with the imported Californian material, whilst the remainder were wholesale and retail nurseries. In 2005, no *P. ramorum* was detected during a national survey but trace-back/trace forward activities found the pathogen on two sites in British Columbia. As of October 2006, eradication efforts were still underway at one of these sites and also at three other nurseries in British Columbia (Anon., 2006a). To date, the pathogen has not been found in Canadian forests and is still under official control in Canada.

Most infected plants in the US are associated with the A2 mating type of what was known as the North American population, although several infections with the A1 mating type of the European population (EU1) have been reported in nurseries (Hansen *et al*., 2003; Osterbauer *et al*., 2004). A2 isolates belonging to the third lineage (NA2) have been found in or traced back to nurseries in Washington State (Ivors *et al*., 2006). Isolates of the NA2 lineage have also been detected in nurseries in Sacramento and San Luis Obispo Counties, USA. (C. Blomquist, *personal communication*).

Central America: No record

South America: No record

Caribbean: No record

Europe: As a result of emergency legislation (Anon., 2002; Anon., 2004), EU Member States have been required to conduct surveys for the pathogen. The results of such surveys from 2004 to 2006 are presented in a tabular form in Appendix 3. These surveys suggest that the pathogen has a restricted distribution in Belgium, Denmark, Estonia, Finland, France, Germany, Ireland, Italy, Luxembourg, Netherlands, Poland, Slovenia, Spain (including Mallorca), Sweden, and the UK. CABI (2007) also reports the pathogen as present in Norway, Switzerland and the Channel Islands (Jersey and Guernsey). Surveys are also required in 2007 (Anon., 2007a). As part of the EU Member State surveys the pathogen has been confirmed absent in Austria, Cyprus, Hungary, Latvia, Lithuania, Malta, Portugal and Slovakia. The pathogen was found in the Czech Republic on imported *Viburnum* plants in 2003, but this outbreak was considered eradicated as further surveys in 2004 and 2005 did not detect the pathogen (Běhalová, 2006).

Although the species was not formally described at the time, *P. ramorum* was first found on *Rhododendron* species in Germany and the Netherlands as far back as 1993 (Werres *et al*., 2001). In Europe, the pathogen is mainly present in non-tree hosts grown in containers located at nurseries and retail garden centres. However, in several countries (including Germany, Ireland, Luxembourg, the Netherlands, Norway, Spain, Switzerland and the UK) some infected plants have been found outside nursery situations in managed parks and gardens and/or in wild (woodland) situations. Infected trees have been found in the UK and the Netherlands. The pathogen is under official control wherever it is found in Europe although in some areas of the UK and the Netherlands only containment measures are being applied, but with a view to attempted eradication. In the UK this includes clearance of infected rhododendron, especially invasive *R. ponticum*.

For the UK, between April 2002 and June 2007, there have been 558 nursery outbreaks at 475 sites across England and Wales. The pathogen has been eradicated from 459 of these outbreaks. In natural and semi-natural environments, there have been 185 outbreaks across 166 sites in England and Wales; eradication efforts have so far been successful for 60 of these outbreaks (D. Slawson, *personal communication*). The 91 infected trees (up to

October 2007) were all located in Cornwall (Joan Webber, *personal communication*), except for an American southern red oak tree (*Quercus falcata*) in West Sussex, which was also the first tree found affected in the UK in October 2003 (Brasier *et al*., 2004a). In late October 2007 a single beech tree (*F. sylvatica*) was found at a managed garden site in West Yorkshire (D. Slawson, *personal communication*). In Scotland, between 2002 and 2007, there have been 34 outbreaks at 23 sites; these have all been on nurseries or garden centres except one outdoor finding (garden/landscape) in 2002 and one in 2007. No findings occurred in 2006 and so it was thought that the pathogen could be considered eradicated (Schlenzig, 2007); however, in 2007, two new nursery findings were made in addition to the one outdoor find (C. Greenslade, *personal communication*). The pathogen has also been observed on *Rhododendron* and *Viburnum* at a number of nursery sites in Northern Ireland (RAPRA EU Project Database, ((http://rapra.csl.gov.uk), undated), and on *Rhododendron* at two sites outside of nurseries in 2007 (A. McCracken, personal communication) .

To date, the majority of isolates tested in Europe have been of the A1 mating type. However, the A2 mating type was identified from *Viburnum bodnantense* in Belgium (Werres and De Merlier, 2003) in 2002 and was confirmed as belonging to the European (EU1) population of *P. ramorum*. Since that initial finding, two further A2 isolates of the European population have been found in Belgium as part of a screening exercise of 280 Belgium isolates collected between 2002 and the end of 2006 (K. Heungens, ILVO, *personal communication*, 2007). Both of the isolates originated from nurseries in northern Belgium from two separate sites and from different hosts, with a 2002 isolate from viburnum and an isolate from the rhododendron in 2003.

Asia: No record

Africa: No record

Oceania: No record

EU: Recorded as present in Belgium, Denmark, Estonia, Finland, France, Germany, Ireland, Italy, Luxembourg, the Netherlands, Poland, Slovenia, Spain (including Mallorca), Sweden and the UK including the Channel Islands (Jersey and Guernsey). The pathogen has been confirmed absent in Austria, Cyprus, the Czech Republic (1 import interception eradicated), Hungary, Latvia, Lithuania, Malta, Portugal and Slovakia. There are no reports on the status of *P. ramorum* in Greece, Bulgaria and Romania (the latter two only joined the EU in 2007). However, *P. ramorum* has never been recorded as present in these countries.

EPPO region: Recorded as present in Belgium, Denmark, Estonia, Finland, France, Germany, Ireland, Italy, Luxembourg, Netherlands, Norway, Poland, Slovenia, Spain (including Mallorca), Sweden, Switzerland, the UK including the Channel Islands (Jersey and Guernsey). The pathogen has been confirmed absent in Austria, Cyprus, the Czech Republic (1 import

interception eradicated), Hungary, Latvia, Lithuania, Malta, Portugal and Slovakia.

The pathogen has not been recorded in the following EPPO member countries: Albania, Algeria, Belarus, Bulgaria, Croatia, Greece, Israel, Jordan, Kazakhstan, Kyrgyzstan, Macedonia, Moldova, Morocco, Romania, Russia, Serbia and Montenegro, Tunisia, Turkey, Ukraine and Uzbekistan.

Origin of *Phytophthora ramorum*: The geographical origin of *P. ramorum* is still a matter of speculation. The recent discovery of the pathogen suggests that it was introduced relatively recently into both North America and Europe from an unidentified third country or countries.

The distribution of mating types provides evidence for the exotic origin of the pathogen. *Phytophthora ramorum* is heterothallic and therefore requires both mating types (A1 and A2) to be present for sexual recombination to occur. It is assumed that both mating types are present in areas where the organism evolved. Therefore, when heterothallic *Phytophthora* species are first introduced outside their natural range, it is not unusual for only one mating type to be initially observed within an introduced population.

When *P. ramorum* was first discovered, only one mating type could be observed in either North America or Europe. The European population was of the A1 mating type whilst the North American population was the A2 mating type. This indicated that the pathogen was likely to have been introduced separately to each continent from an area or areas where both mating types were present. However, since these initial findings the A2 mating type has been found in Europe, albeit only three times in Belgium; these A2 isolates all belonged to the European lineage. Also, A1 isolates have been found in nurseries in Oregon and Washington (Ivors *et al*., 2006), and these are related to the European population, suggesting an introduction either from Europe or from an unidentified third country origin.

Other genetic evidence supports the theory that the pathogen was introduced separately to both continents. Genetic profiling by analysing Amplified Fragment Length Polymorphisms (AFLPs) indicates that the North American population is largely clonal (Ivors *et al*., 2004), whilst the European population consists of an array of mainly unique, closely related, AFLP types (Ivors *et al*., 2004). Single nucleotide polymorphisms exist in the *coxI*, β-tubulin and cellulose binding elicitor lectin genes between the North American and European population (Kroon *et al*., 2004; Bilodeau *et al*., 2004), as do differences in growth rate, colony morphology and pathogenicity (Brasier *et al*., 2004b).

Recently, an analysis of genetic variation using micro-satellite markers indicated there was significant genetic variation between European and North American isolates (Ivors *et al*., 2006). The study confirms that the North American genotypes are very closely related and suggests a single genotype introduction confirming the exotic nature of the pathogen. The micro-satellite study also confirmed that genetic diversity amongst European isolates was

slightly higher, suggesting the introduction of a few closely related genotypes followed by the creation of new genotypes via mitotic recombination and/or mutation.

The evidence discussed above supports the exotic nature and separate introductions of the pathogen, but gives few clues as to the geographical origin. The closest relative of *P. ramorum*, based on analysis of ribosomal DNA Internal Transcribed Spacer (ITS) sequences and MtDNA sequences are *Phytophthora lateralis* and *Phytophthora hibernalis* (Werres *et al*., 2001; Martin *et al.,* 2004). *Phytophthora lateralis* is an invasive pathogen affecting *Chamaecyparis lawsoniana* in Oregon and northwestern California, but is believed to have originated from Asia (E. Hansen, *personal communication* as cited by Brasier *et al*., 2004b). Brasier *et al*. (2004b) suggests that *P. ramorum*, like *P. lateralis*, may have originated in forested areas of Asia where, having co-evolved with native hosts, it is relatively benign in its natural habitat. Brasier *et al*. (2004b) goes on to suggest that Yunnan, Taiwan and the eastern Himalayas may be likely areas of origin for *P. ramorum*. Yunnan was mentioned in particular, due to its vegetation, climate and for being a popular destination for plant collectors. Goheen *et al*. (2005) were unable to detect *P. ramorum* at four forestry sites they visited in Yunnan province. However, an abundance of *P. ramorum* host genera were present and foliar and dieback symptoms similar to those caused by aerial *Phytophthora* species were observed.

DETECTION AND IDENTIFICATION

Symptoms

Due to the large number of hosts that have been naturally infected, a comprehensive description of symptoms for each one is not given here. However, the types of symptoms observed for each host are listed in Appendix 1, and are illustrated in the Defra *P. ramorum* leaflet (Defra 2006d.). Essentially, three disease types have been recognised (Hansen *et al*., 2002): ramorum bleeding canker, ramorum dieback and ramorum leaf blight.

Ramorum bleeding canker, also referred to as Sudden Oak Death in the USA, refers to bleeding trunk cankers often associated with tree mortality; ramorum dieback refers to leaf and shoot/stem infections which result in dieback; ramorum leaf blight is where infection is restricted to the plant foliage only. In the case of trees, individual species may develop just bark cankers, both bark cankers and leaf and/or shoot infections, or leaf infections only. In the USA, tanoak (*L. densiflorus*) is an example of a host where both bark cankers and leaf/shoot infections occur; all aerial parts of the tree can be affected (leaves, shoots, twigs, branches, stems, trunks). In the UK, sweet chestnut has exhibited both bleeding cankers and foliage infections. On *Q. ilex* (holm oak) in the UK, only leaf symptoms have been observed to date even although bark susceptibility has been demonstrated in experimental log tests; other trees have also only shown foliage infections, e.g. ash (*F. excelsior*).

Both the importance of root infection by *P. ramorum,* and its incidence in natural infections is yet to be determined; typically in California, trunk lesions do not appear to extend below ground level. However, three seedlings of tanoak (*L. densiflorus*) with symptoms have been shown to have root infections. Parke *et al*. (2006) observed seedlings and saplings of *L. densiflorus* with unusual symptoms on the lower leaves including dark discolouration of the mid-veins and petioles. However, the upper leaves had a healthy appearance. On the trees with the unusual symptoms, the pathogen was isolated from the roots.

Root infection has not been reported for mature trees or in established/wild shrub species. The pathogen has not yet been isolated from oak roots (*Quercus* spp.) although it has recently been isolated from above-ground root flares of beech (*F. sylvatica*) in the UK (J. Webber, *personal communication*).

Root colonisation has been reported experimentally on potted rhododendron plants where potting media was inoculated with *P. ramorum*. Plant mortality occurred within 3 to 7 weeks and the pathogen could be detected within the cortex and vascular tissues of the roots and stems (Parke & Lewis, 2007). Sporangial drenches of roots of living plants of a range of species and isolation after a month, led to recovery of *P. ramorum* from the roots of 12 out of the 14 species tested(Shishkoff, 2007).Lewis *et al*. (2004) observed symptoms on three-year-old *Rhododendron* 'Nova Zembla' plants but the full symptoms were not described by the authors. Colburn *et al*. (2005) inoculated roots of *Rhododendron* 'Cunninghams White' plants and while the root systems appeared healthy afterwards, the pathogen could be isolated from the roots. Shishkoff and Senesac (2005) inoculated several weed species and isolated *P. ramorum* from the roots of *Epilobium ciliatum* (American willow herb) despite surface sterilisation, this suggested that the roots were colonised internally by *P. ramorum*. All of these studies suggest that *P. ramorum* has the potential to infect roots of a range of hosts and this may be a mode by which the pathogen is moving in the nursery trade.

P. ramorum has been isolated from rotting roots of *Viburnum* plants in the UK with basal stem cankers (C. Lane, *personal communication*). It is not clear whether the pathogen extended into the roots from the basal stem canker stem, or *vice versa*.

Pathogen morphology

The following section is compiled from Werres *et al*. (2001), Brasier and Kirk (2004), Werres and Zielke (2003), and Anon. (2006b). Colonies vary dependent upon growth media. On carrot piece agar, cornmeal agar and V8 juice agar, colonies are submerged with little or no aerial mycelium. Concentric rings are usually clearly visible. On cherry decoction agar appressed aerial mycelium and an indistinct rosette pattern are visible. Hyphae are up to 8 µm wide. Table 1 describes the appearance of the colonies of the three lineages EU1, NA1 and NA2 on V8 agar.

Sporangia are produced individually or in clusters of 2–12 (rarely 16) and are arranged sympodially on long sporangiophores. They are mostly ellipsoid, spindle or elongated oval shaped with a rounded base, though occasionally bases are tapered. Lengths and widths are 25–97 x 14–34 µm with an average length: width ratio of 1.8–2.4. Sporangia are semi-papillate with one narrow papilla (5–8 µm). Zoospores are produced in sporangia in water at temperatures below 20ºC. Sporangia germinate directly at higher temperatures.

Chlamydospores are globose, mostly thin-walled, intercalary or terminal, (occasionally laterally produced) 20–91 µm diameter. Chlamydospores are more common in older colonies and hyaline to pale brown or brown in colour.

P. ramorum is heterothallic and oogonia only develop in dual cultures where isolates of opposite mating types are present. When produced they are terminal, often laterally sessile, smooth and nearly spherical 24–40 µm diameter. Oospores are 20–36 µm in diameter and plerotic. Antheridia are amphigynous and approximately 12–22 x 15–18 µm. To date, oospores have never been seen in nursery stock or field-grown plant material but they have been produced experimentally.

Isolates of the North American population are slower growing and more phenotypically variable than those of the European subpopulation (Brasier *et al*., 2002; Zielke and Werres, 2002; Ivors *et al*., 2006).

Detection and inspection methods

On trees, *P. ramorum* infection is associated with dead bark (phloem) and cambium on the lower trunk, sometimes with discoloured wood (xylem) below the lesions up to a depth of 25mm (Brown and Brasier, 2007). Oozing globules of dark-reddish or black liquid may also be seen from affected areas. On *Rhododendron* and other ornamental species, symptoms include discoloured areas on twigs, dark brown lesions on leaves and wilting. For a full list of affected hosts, together with details of symptoms, please see the table of natural hosts in Appendix 1.

Sampling and diagnostic procedures are described in the EPPO standard for diagnostics PM 7/66(1) (Anon., 2006b); similar schematics are detailed by the USDA and these include diagnostic protocols as well as sampling protocols for plant material, soil, growing media and water. (http://www.aphis.usda.gov/plant_health/plant_pest_info/pram/protocols.shtml).

Isolation

P_5ARP[H] media is most commonly used for isolation as it is semi-selective for *Phytophthora* species; characteristic morphological features can be readily observed. Isolation from both water and soil utilises a *Rhododendron* leaf bait test (Themann *et al*., 2002). This method was adapted for use to detect *P. ramorum* in UK watercourses (Defra, 2007a): muslin bags containing leaf

pieces of *Rhododendron catawbiense* were placed in various watercourses for three days; presence of *P. ramorum* could then be determined either by direct isolation onto P_5ARP[H] media, or by real-time polymerase chain reaction (PCR) (see below). Isolation is generally reliable, but can be affected by the host species (e.g. the pathogen may not be readily isolated from certain hosts), tissue type (e.g. bark lesions can be harder to isolate *P. ramorum* from than leaf tissue for some hosts), or season (e.g. in California, it is often difficult to isolate the pathogen during the hot, dry summer months). Compared to PCR, isolation has the advantage of confirming the viability of the pathogen.

Serological methods

These have been utilised as a preliminary screen for the presence of the genus *Phytophthora* using genus-specific antibodies in an ELISA format. Bulluck *et al*. (2006) reported the use of an enzyme-linked immunosorbent assay (ELISA) to detect *P. ramorum* from camellia leaves; the ELISA method is incorporated as an option in the USDA diagnostic protocol. The advantage of ELISA is that is cheap and easy to use as a primary screen when dealing with a large numbers of samples; however, currently only genus-specific antibodies are available, so positive samples need additional confirmatory tests using more specific methods (e.g. isolation or PCR). Lateral flow devices (LFDs), also known as immunochromatographic assays, have also been designed that are *Phytophthora* genus specific and these can be used in the field. Lane *et al*. (2006) reported the use of these LFD kits by Defra's Plant Health and Seed Inspectorate (PHSI) for on-site testing and in a comparative trial, performed relatively well against laboratory-based methods. Out of 634 samples, 84.5% tests gave correlated results, 11% false positives and 4.4% false negatives. The diagnostic sensitivity was 87.6% and the diagnostic specificity was 82.9% (Lane *et al*., 2007). The LFD kits are available commercially (Pocket Diagnostics ™ and Neogen Europe Ltd).

DNA-based molecular methods

Several molecular tools for the diagnosis, detection and analysis of *P. ramorum* including PCR, amplified fragment length polymorphisms (AFLP) and restriction fragment length polymorphisms (RFLP) have been developed (Bilodeau *et al*., 2002; Bonants *et al*., 2002; Hayden *et al*., 2002; Ivors *et al*., 2004; Kong and Hong, 2002; Kox *et al*., 2002; Kroon *et al*., 2004; Martin *et al*., 2002; Martin *et al*., 2004; Martin and Tooley, 2004; Kong *et al*., 2004; Prospero *et al*., 2004; Ioos *et al*., 2006). Several real-time PCR assays have also been designed from the spacer region of mitochondrial *coxI* and *coxII* genes or the ITS region of ribosomal DNA. These utilise both TaqMan (Hayden *et al*., 2006; Tooley *et al*., 2006; Uribe, 2005; Bulluck *et al*., 2006; Hayden *et al*., 2004; Bilodeau *et al*., 2004; Hughes *et al.*, 2006a; Defra, 2005b; Sechler *et al*., 2006) and SYBR green techniques (Uribe, 2005). Schena *et al*. (2006) report a real-time multiplex TaqMan PCR that can be used to simultaneously identify *P. ramorum* and three other *Phytophthora* species using a set of primers designed from introns of the *Ypt*1 gene. PCR methods are generally very specific and sensitive.

All these assays can be used to identify DNA from pure culture; some can be used for direct detection and identification *in planta*, though this may depend on the host and the ability to extract high quality DNA from the substrate. Sechler *et al*. (2006) reported that their assay was sensitive enough to detect DNA from one *P. ramorum* chlamydospore in 250 mg of potting media or forest soil. The assay of Hughes *et al*. (2006a) has been adapted for on-site use (Tomlinson *et al*., 2005), by utilising a rapid and simple DNA extraction method with a portable real-time PCR platform (Cepheid SmartCycler II). This was successfully used for the detection of *P. ramorum* causing dieback of ironwood (*Parrotia persica*) at a managed garden site in the UK (Hughes *et al*., 2006b). This real-time PCR assay can also be used to detect the presence of the pathogen prior to the development of symptoms in *Rhododendron, Viburnum* and *Camellia* plants (Defra, 2007b) and has been deployed occasionally at points of entry into the UK to test imported material. Real-time PCR assays developed by CSL have been used to quantify *P. ramorum* DNA in soil and water (Turner *et al*., 2007). However, all the molecular assays mentioned above, detect the presence of pathogen DNA and not the presence of a viable pathogen. A real-time PCR assay has been designed with the use of messenger RNA as a viability marker, on the basis of its rapid degradation compared to DNA (Chimento and Garbelotto, 2007). *Phytophthora ramorum* specific primers for this assay were designed in the cytochrome oxidase gene encoding subunits I (c*oxI*).

BIOLOGY

P. ramorum produces vegetative hyphae and four types of spores: sporangia, zoospores, chlamydospores and oospores; all but oospores are found to occur in nature to date.

Life cycle

Hyphae

Hyphae grow within infected tissue and gain nutrition necrotrophically. The pathogen can also gain nutrition saprophytically but is not considered to be significantly competitive with other micro-organisms. The persistence of hyphae/mycelium in host tissue is unknown, but it does not appear to be adapted for survival or competition.

Sporangia

These are sometimes called zoosporangia and are produced asexually. They are produced on leaf lesions (and green shoots of some hosts) from specialised hyphae called sporangiophores emerging through stomata or wounds/ruptures. Sporangia are deciduous and their primary function is dispersal. Sporangia release motile zoospores (infective spores) in moisture; some (particularly older sporangia) may not produce zoospores, but may germinate directly to produce mycelium (which may then produce further sporangia). On agar media, sporangia may aggregate in clusters, and do not

shed even when violently shaken or subjected to strong air humidity changes (Moralejo *et al*., 2006a).

Zoospores

These are motile flagellate spores that are released from sporangia under cool, moist conditions. They can swim for a considerable time before encysting. Once discharged, they can be dispersed further by rain-splash. Zoospores encyst and then typically germinate to infect the host. Moralejo *et al*. (2006a) observed repetitional diplanetisim amongst zoospores of *P. ramorum* in laboratory conditions. Repetitional diplanetisim is the formation of a swimming zoospore from a zoospore cyst. The high frequency of repetitional diplanetisim *in vitro* suggests that this may not be rare in nature and zoospores cysts may therefore have a limited survival role. Zoospores of *P. ramorum* appear to be negatively geotropic; in spore suspensions they tend to aggregate at the water surface.

Chlamydospores

These large, thick-walled spores have a major role in survival. They are produced asexually in infected leaf and (possibly) shoot tissue; they are also reported to occur in bark phloem and xylem tissue of tanoak (*L. densiflorus*) (Parke *et al*., 2007). The tissue in which these are formed can vary with the host; they can also be formed on mycelium growing out of leaf lesions but are apparently not as readily detached as sporangia. Chlamydospores formed within rhododendron leaves are smaller with thicker walls than those formed *in vitro* and reach their maximum size in 10 days (Smith and Hansen, 2007). Smith and Hansen (2007) also reported that chlamydospores germinate slowly *in vitro*, at a low but highly variable frequency, with smaller chlamydospores germinating more frequently than larger ones. Chlamydospores typically germinate to produce hyphae and sporangia.

Oospores

Oospores are the sexual spores of *P. ramorum* and may be formed when both A1 and A2 mating types are present. Oospores can be produced in culture and in host tissue (rhododendron stems) in the laboratory, but whether they can be produced in nature is still unknown, as it depends upon the presence of opposite mating types in the same environment and a functional mating system (see below). In Europe, only three isolates of the A2 mating type have been found (K. Heungens, *personal communication*), in Belgium, so there will have been only very limited opportunity for any potential sexual reproduction and the production of oospores. In North America a limited number of European A1 isolates have been found on nursery stock (Hansen *et al*., 2003; Osterbauer *et al*., 2004). Whether sexual reproduction has occurred in the field as a result of the presence of both mating types is not known. Generally for *Phytophthora* species, oospores are considered to be thick walled and have a potential role in long-term survival. Sexual reproduction also serves to increase genetic diversity and adaptation of the pathogen. However, the

importance of oospores with regards to survival and sexual reproduction for *P. ramorum* is still unknown.

There is still some uncertainty regarding the capacity of *P. ramorum* for sexual reproduction. Laboratory pairings of the A1 and A2 isolates have resulted in the slow production of gametangia, which were in low numbers and not well formed (Defra, 2005a; Brasier, 2003; Brasier and Kirk, 2004). Werres and Zielke (2003) found that the most successful partners *in vitro* for stimulating gametangial production were as follows: for the North American A2 isolates, *Phytophthora cryptogea* and *Phytophthora cambivora*; for the European A1 isolates, *P. cryptogea* and *Phytophthora cinnamomi*. They also observed that most oospores were formed on living rhododendron stems indicating that the host-pathogen interaction may aid the formation of gametangia.

As part of a study on the functionality of the *P. ramorum* mating system, Werres *et al*. (2007a) attempted the induction of gametangial formation and oospore production between European and North American isolates. They assessed over 900 *P. ramorum* gametangia induced by pairing European A1 (EU1) and North American A2 (NA1 and NA2) *P. ramorum* isolates. They found that a high frequency (average *ca.* 57%) of gametangia were abnormally developed or contained visibly aborted oospores. Using tetrazolium staining, around 9–77% (average *ca.* 30%) of *P. ramorum* gametangia contained apparently viable but often thin-walled oospores. In their tests, pairings between European A1 (EU1) and European A2 (EU1) were also set-up but no oogonia or oospores developed.

Studies at CSL have found that pairings of European A1 (EU1) isolates with North American A2 (NA1) isolates resulted in the formation of oospores (P. Giltrap, *personal communication*) but it was not possible to get them to germinate. Also, the two most recently discovered European A2 isolates from Belgium (EU1) consistently produced oospores when paired with other European A1 isolates (EU1) but not when paired with US A2 isolates (presumed to be NA1) (K. Heungens, *personal communication*). However, attempts at germination of the oospores were unsuccessful.

Whether the mating system of *P. ramorum* is fully functional is still uncertain, but if it is, then it increases the potential for genetic diversity to occur should opposite mating types come together. It has also been proposed that even without A1 × A2 mating, genetic recombination might occur via zoospore fusion between EU1 and NA1 lineages (Brasier, 2007).

Disease cycle

The lifecycle and disease cycle are central to understanding the epidemiology of *P. ramorum*. Each component part of the pathogen's epidemiology is presented below.

Asexual sporulation and germination of *Phytophthora* species are reviewed by Judelson and Blanco (2005); information on other general aspects of the epidemiology of *Phytophthora* species can be found in Erwin & Ribeiro, 1995.

Asexual spore production

Laboratory studies

Sporulation can be affected by a variety of biotic and abiotic factors, including host, temperature, light and moisture. *In vitro* studies by Englander *et al*. (2006) have shown that sporangia were produced at temperatures ranging from 6 to 26°C, with an optimum of 22°C for the three European isolates tested. For the four North American isolates tested sporangial production occurred over a broader range of temperatures (10–30°C) and the optimum temperature varied with each isolate, but optima ranged from 16 to 22°C. Light was also shown to affect sporulation in this study, North American isolates were shown to grow less and produce fewer sporangia when exposed to increasing doses of near-UV radiation (50–300 μW/cm^2) and visible radiation (250–1500 μW/cm^2). European isolates were only exposed to 300 μW/cm^2 and, whilst growth was affected for one isolate of the three tested, there was no effect on spore production.

The effect of temperature and humidity on sporulation was investigated under laboratory conditions by Turner and Jennings (2006). Differences in humidity had most effect on sporangial production and zoospore germination whereas sporangial germination was less sensitive. Maximum levels of sporangial production and zoospore germination occurred at 100% humidity and temperature optima for sporulation and germination ranged from 20 to 30°C depending upon experimental conditions.

Temperature significantly affected the production of zoospores from California bay laurel (*U. californica*) leaves in laboratory trials (Davidson *et al*., 2005). Zoospores were produced at all temperatures (5, 10 15, 20 and 25°C) but not at 30°C. In the first trial, the number of zoospores produced at 15°C was significantly higher than the numbers produced at 5, 10 and 25°C. The number of zoospores produced at 20°C was significantly higher than the number produced at 5°C, and tended to be higher than the numbers produced at 10 and 25°C. Less differences were observed when the experiment was repeated, with only the 25°C treatment producing significantly higher numbers of zoospores than the 5°C treatment. However, the number of zoospores produced at 15 and 20°C still tended to be higher than the numbers produced at 5 and 10°C.

Foliar (and/or green shoot) infections can support the production of sporangia and/or chlamydospores, though production of both spore types varies markedly with the host:

In US experiments with inoculated detached leaf discs of various hosts, the capacity of *P. ramorum* to produce sporangia, zoospores and chlamydospores was greatest and most rapid on California bay laurel (*U. californica*). Tanoak (*L. densiflorus*) also supported the production of numerous sporangia and zoospores soon after infection; shoots sporulated more prolifically than leaves (J. Parke, 2002, *personal communication*). On

madrone leaf disks (*A. menziesii*), only chlamydospores were produced. On wild *Rhododendron* and evergreen huckleberry (*Vaccinium ovatum*) a few to many sporangia were produced over the course of several days. Of species not reported as natural hosts, inoculum production was abundant on vine maple (*Acer circinatum*) and salal (*Gaultheria shallon*) (Parke *et al*., 2002a).

UK studies using detached leaf assays have shown that different 'leaf' hosts have different sporulation potentials (Defra, 2005c). *Syringa vulgaris* (lilac), *U. californica* (California bay laurel), dog rose (*Rosa canina*) and *V. myrtillus* (bilberry) produced the highest amounts of sporangia; *R. ponticum, F. excelsior* (ash) and *Camellia japonica* were moderate producers of sporangia. Some hosts produced negligible numbers of sporangia, e.g. *Vaccinium vitis-idaea* (cowberry) and *Arctostaphylos uva-ursi* (bearberry). This study did not quantify sporulation of different hosts outdoors, but rhododendron (especially *R. ponticum*) appears to be the key sporulating host in UK outbreaks on established plants (parks, managed gardens and wild sites); many infected trees have been associated with infected *Rhododendron* (Brasier and Jung, 2006; Brown *et al*., 2006a). In addition to the number of spores produced in laboratory tests over a specific period of time, the overall duration of spore production and total numbers produced under natural environmental conditions may be significant.

Chlamydospore production was generally less abundant than sporangial production on the hosts tested in one UK detached leaf study (Defra, 2005c). Chlamydospores were produced on less than half of the 17 host species with the highest levels recorded on lilac (*S. vulgaris*), only slightly higher than the number produced on California bay laurel (*U. californica*). In comparison, *Viburnum opulus* and ash (*F. excelsior*) supported production of relatively moderate numbers of chlamydospores whereas production on *R. ponticum* was low. Of the heathland species tested, *Vaccinium myrtillus* (bilberry) supported significant numbers of chlamydospores.

In detached leaf assays to determine sporulation on the leaves of tree species in the UK (Denman *et al*., 2006), it was found that ash (*F. excelsior*) and lilac (*S. vulgaris*) supported consistently high sporulation, whilst significantly fewer sporangia were observed on horse chestnut (*A. hippocastanum*) and sessile oak (*Q. petraea*). In tests on *Q. robur* (common or English oak), holm oak (*Q. ilex*), *R. catawabiense* and turkey oak (*Q. cerris*), *Q. ilex* and *R. catawabiense* all supported more sporangia than the two other oak species (*Q. robur* and *Q. cerris*) which are not recorded naturally as foliar hosts.

Moralejo *et al*. (2006b) observed that additional multi-hyphal structures were present when they inoculated some woody Mediterranean plants with *P. ramorum*. These plants were *Arbutus unedo* (strawberry tree), *Ceratonia siliqua* (carob bean), *Laurus nobilis* (bay laurel), *Pistacia lentiscus* (mastic), *Rhamnus alaternus* (Italian buckthorn) and *V. tinus*. Stromata (cushion like masses of hyphae) were consistently formed on fruit and leaves of several Mediterranean shrubs. Occasionally sporangia and chlamydosori (packed clusters of chlamydospores) were formed on the stromata.

Field studies

Biotic factors have also been shown to affect sporulation of *P. ramorum* in the field, e.g. tissue type (e.g. leaf versus bark) and host species. With respect to tissue type, lesions on mature tree bark are not considered to produce sporangia and are therefore not considered a significant source of inoculum (Davidson *et al.* 2002a; Defra, 2005c). Although sporangia have been observed in ooze from bleeding trunk cankers, they are considered to be external contaminants. In an observational study in California on infected coast live oaks (*Q. agrifolia*) and tanoaks (*L. densiflorus*) by Tjosvold *et al*. (2002a), sampling and testing the ooze for presence of the pathogen, less than 2% of the isolations attempted were positive, and no spores were observed in the ooze. Davidson *et al*. (2005) tested the surfaces and exudates of cankers of infected *Q. agrifolia* bark and no *P. ramorum* could be found.

In California, tanoak and California bay laurel are considered to be the main producers of *P. ramorum* inoculum in tanoak-redwood woodlands. In mixed evergreen woodlands, where coast live oak (*Q. agrifolia*) and California bay laurel (*U. californica*) are dominant species, California bay laurel is considered the main generator of inoculum (Davidson *et al*., 2005). California bay laurel is significantly represented in the plant species composition of these woodland habitats and is present as both an under-storey and over-storey species, being a tree that can reach 30–40m in height. Sporangia are also produced on infected shoots/leaves of tanoak (*L. densiflorus*) and this is also a significant source of inoculum in tanoak-redwood forests. Spore production on this host is on infected shoots and leaves. *Rhododendron macrophyllum* (Pacific rhododendron) is also considered a significant spore-producing host, but it produces lower numbers of sporangia than California bay laurel or tanoak shoots/leaves.

In California's Mediterranean-type climate, sporangia on California bay laurel are first produced several months after the beginning of the rainy season, i.e. winter/spring and reach a peak at the end of the rainy season, which is usually April/May (Davidson *et al*., 2002a; Maloney *et al.*, 2002). (N.B. The rainy season runs from October to April in northern California and from November to March or April in southern California). Sporangial production tends to occur earlier (December/January) in tanoak-redwood woodlands than mixed-evergreen forest (e.g. coast live oak – Californian bay laurel woodlands) where there appears to be a lag of several months (D. Rizzo and J. Davidson, 2004, *personal communication*). This is for two main reasons: infected California bay laurel leaves are not shed as much in the wetter, cooler tanoak-redwood woodlands (Davidson *et al.*, 2002a); and lesions on California bay laurel leaves remain more active/viable in tanoak-redwood woodlands after the hot summer period than in coast live oak woodlands (Davidson *et al.*, 2002a; D. Rizzo, *personal communication*). As well as seasonal variation in spore production, variation also occurs from year to year. High levels of disease in some years are attributed to high levels of winter/spring rainfall, which then extends into early summer (April/May). Annual variation in rainfall can also influence sporulation (Davidson *et al*.,

2005). A twenty-fold increase in sporangial production compared to pre-rain levels was observed during late rains in spring 2003 in a mixed evergreen forest in California. These data point to the potential importance of climatic events such as El Niño (which can result in increased rainfall along the central California Coast) in influencing the establishment and spread of the pathogen (Rizzo *et al*., 2005). The epidemic mortality on coast live oak (*Q. agrifolia*) trees one to two years after the 1998 El Niño is an example of this (Davidson *et al*., 2005). The pattern was repeated in 2005-2006.

In summary, sporulation on infected foliar hosts plays a key role in the epidemiology of *P. ramorum* in forests and woodlands by serving as a source of inoculum to trees.

Means of movement and dispersal

Local dispersal

Sporangia are caducous (deciduous), i.e. they can detach from the sporangiophore. Sporangia of *P. ramorum* are thought to require water to dislodge (Moralejo *et al*., 2006a). Local dispersal of *P. ramorum* is by splash-dispersed sporangia/zoospores that are produced on infected leaves/shoots. Sporangia are thought to be the primary means of local dispersal for *P. ramorum*. For *Phytophthora* species in general, sporangia may be dispersed in water or aerially over long distances in favourable conditions such as during thunderstorms (Goodwin, 1997), depending on the species and their dispersal strategies. For *P. ramorum*, sporangia were initially considered to have the potential to be dispersed in wind-blown mists. Despite *P. ramorum* being a caducous species, sporangia are relatively difficult to detach, at least in experiments. Using electric fans, sporangia remained attached and shrivelled rapidly (J. Davidson, 2004, *personal communication*). Moralejo *et al*. (2006a) found that sporangia do not shed even when violently shaken or subjected to strong air humidity changes.

Mist may create more optimum conditions for disease development by elevating the humidity. When canopies become saturated by rain, dew, or mist, large water drops can form on the leaves, under canopies drip splash may be as important for the spread of fungal pathogens as direct rain splash (Fitt *et al*., 1989). Davidson *et al*. (2005) found that in mixed evergreen woodlands in California (coast live oak-California bay laurel woodlands), inoculum could be dispersed horizontally up to 15m away from the Californian bay laurel trees at the edge of glade. However, this was relatively rare and the findings at 5m and over were all associated with rain events. Most inoculum was trapped at 0m (40% rain traps positive for *P. ramorum*) and 5m (15% positive). Less inoculum was trapped at 10m (10% positive) and only one trap at 15m was positive (less than 2%). In Oregon (Brookings, Curry County), clustering of infection also suggests local dispersal (E. Hansen, 2004, *personal communication*), though infection is most often in the tanoak (*L. densiflorus*) canopy. It was found that 24% of newly infected trees were with 24 feet of previously infected trees; 47% were within 100 feet; 80% were within 300 feet; but one newly infected tree was *ca.*10, 000 feet from any

previously known infected tree. There was some suggestion of spread in a south to north direction in the direction of the prevailing wind and against the general drainage slope (E. Goheen and E. Hansen, 2004, *personal communication*).

From these data it would appear that the pathogen spreads around woodland through repeated local dispersal of secondary inoculum from one proximal host to another. Rarer long-distance spread via a 'turbulent air' mechanism is also considered to occur and allows 'jumps' from one area of infected woodland to another (Hansen *et al*., 2007). There is good evidence that foliar hosts play a key role in the epidemiology of *P. ramorum* in US forests by serving as a source of inoculum for tree cankers (Davidson *et al*., 2002a; Davidson *et al*., 2003; Davidson *et al*., 2005). Kelly and Meentenmeyer (2002) showed that abundance of California bay laurel (*U. californica*) is an important explanatory factor for the pattern of oak mortality through stem cankers in Californian forests. Observations of infections of California bay laurel and oak trees in California forests by Rank *et al*. (2007) have also led them to suggest that *P. ramorum* spreads among California bay laurel in advance of infection on canker hosts, which emphasises the key role this host plays in the establishment of *P. ramorum* in oak woodland in California.

A similar situation with regard to foliar hosts serving as a source of inoculum for tree stem infections occurs in the European population. However, *Rhododendron* appears to play the main role as the epidemiologically important under-storey plant. Most tree stem infections (bleeding cankers) in the UK and The Netherlands have been associated with infected *Rhododendron* plants. However, relatively few trees have been killed in the UK and the Netherlands compared to California.

Sporulation potential has already been referred to (under '***Asexual spore production***') but is referred to again here because differences in sporulation potential and host species prevalence in woodlands (rhododendron in the UK and California bay laurel and tanoak in North America) may be one factor explaining the differences in tree mortality observed between Europe and North America. European isolates of *P. ramorum* are on average more aggressive, e.g. in tests involving *Q. rubra* and rhododendron, than those originating from North America (Brasier, 2003). Comparative experiments undertaken in the UK (Defra, 2005c) measuring sporangial and chlamydospore production on ornamental and under-storey hosts using detached leaf assays found that leaves of *U. californica* were a prolific producer of sporangia and chlamydospores, more so than *R. ponticum*. Out of 18 species, sporangial and chlamydospore production on *U. californica* was second highest producing 216 sporangia/cm^2 and 978 chlamydospores per leaf whilst *R. ponticum* only produced on average 8 sporangia/cm^2 and 17 chlamydospores per leaf. In this experiment, other woodland species such as dog rose (*Rosa canina*) and horse chestnut (*A. pseudoplatanus*) were prolific producers of sporangia but produced few or no chlamydospores. Incidentally, *Syringa vulgaris* (lilac) appeared to produce the most spores of both types in this experiment, but from extremely large lesions. This, and other experiments (see Appendix 2) showed that lilac is extremely susceptible to *P. ramorum*.

However, naturally infected lilac leaves die soon after infection and therefore may not support repeated inoculum production. Also, *U. californica* leaves may be able to support repeated inoculum production. The average lesion lengths of *U. californica* were only 8 mm compared to 220 mm on lilac leaves. Arnold and Rizzo (2007) have shown that leaves of *U. californica* can support repeated inoculum production in a controlled environment. Sporulation potential is not related to lesion size (Defra, 2005c); the length/duration of spore production is also a significant factor that may be host mediated.

Not all infections in the UK have been associated with direct proximity to rhododendron, some infections appear to be associated with water runoff from branch forks, whilst others are only explained by inoculum dispersal distances of over 50m from the nearest infected rhododendron (Brasier and Jung, 2006). There is evidence from UK monitoring studies for dispersal at a distance of at least 50m from the nearest infected host (Turner *et al*., 2007). Many of the already known methods of movement and dispersal from an infected host, including direct contact, water splash and wind-driven rain are not presently known to disperse the pathogen more than this distance. However, Davidson *et al*. (2005) hypothesised that high winds associated with relatively rare storm events could move spores over greater distances. This has also been suggested by Hansen *et al.* (2007) who hypothesised a turbulent air mechanism.

There is potential for longer means of natural movement of the pathogen via watercourses. Davidson *et al*. (2005) detected dispersal of inoculum in stream water 1 km from an inoculum source. In the UK, *P. ramorum* can be found in watercourses at outbreak sites (Defra, 2007c), though the epidemiological significance of this is unknown. A survey of *P. ramorum* in watercourses was conducted at nine sites throughout England (Defra, 2007a). This was done using a rhododendron leaf bait technique. The majority of positive baits were recovered from one site in West Sussex, which had a history of *P. ramorum*. *Phytophthora ramorum* was also recovered from the river catchment area originating from the West Sussex location. Analysis of these positive findings from the river catchment area showed that inoculum disappeared within a few kilometres downstream of the outbreak source (the West Sussex outbreak site). A few positive findings were also found in two other watercourses from locations that are relatively intensively gardened (in gardens near heathlands in Surrey and Dorset) but the pathogen does not appear to have spread beyond managed gardens. *Phytophthora ramorum* was not detected at the five other sites, which included the North Yorkshire Moors, a Cheshire park, Dartmoor, Thetford Brecklands, and suburban Birmingham, indicating that *P. ramorum* still has a relatively restricted distribution in England.

Monitoring of levels of inoculum in water at one UK site showed that seasonal patterns exist (Turner *et al*., 2007). Highest levels of inoculum, as detected by bait tests, generally occurred in winter and spring and lowest levels in summer. Monitoring of watercourses in the USA has shown similar trends, with reduced detection in the summer months. In California, the pathogen could be detected in water samples taken from streams during the winter/spring but only very rarely during the dry summer months (Tjosvold *et*

al., 2002b). In a separate study using baits placed in California streams (Maloney *et al.*, 2002) detection was reported in both spring and summer months in streams, regardless of any rain event.

Oak *et al*. (2007) conducted a wider survey of watercourses in the USA. Eleven states were surveyed including California and Oregon, along with seven states where the pathogen has only been detected in association with nursery plants and two states where the pathogen has not been detected. The survey found that *P. ramorum* was only detected in regulated areas in California and Oregon and in one stream draining an ornamental plant nursery in Washington where *P. ramorum* has been detected twice previously. In 2007 (to date) thus far there have been three *P. ramorum* positive streams previously thought to be negative (outside areas where the pathogen is endemic). Two have been detected in streams in Washington and one in Mississippi; all are in watersheds where nurseries growing ornamental plants have had infected plants (S. Oak, *personal communication*).

Oregon State has found that the pathogen is regularly recovered from streams draining infested sites, five years after eradication treatment (Sutton *et al*., 2007). The pathogen was first detected using stream baiting in three other watersheds and subsequent ground surveys located infected tanoak (*L. densiflorus*) and other host plants. *Phytophthora ramorum* is yet to be detected from any water sources in Georgia (Williams-Woodward and Adams, 2007), where the pathogen has only been detected in ornamental nurseries and home landscapes.

Sporangia may potentially be spread by insects, although this has not been confirmed, and preliminary investigations have not recovered the pathogen. (McPherson *et al*., 2002). UK studies undertaken between 2003 and 2007 have not detected any indication of disease spread via insect vectors (Defra, 2005c). Bark beetles, such as western oak bark beetle (*Pseudopityophthorus pubipennis*), oak ambrosia beetle (*Monarthrum scutellare*) and the minor oak ambrosia beetle (*M. dentigerum*) have been investigated as potential vectors in the USA (McPherson *et al*., 2000). In a study in Oregon (Kanaskie *et al*., 2002) using vane traps with associated cut logs as baits, *P. ramorum* was apparently not detected from insects in the vane traps or in bait logs; the most frequently trapped insects were *Xyleborinea saxesenii*, *Pseudopityophthorus pubipennis* and *Monarthrum scutellare*. In Oregon, tanoak infections in the crown are often associated with bark beetle holes (E. Goheen and E. Hansen, 2004, *personal communication*), but their role as vectors is not proven and they may simply be targeting infected tissue.

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.* (2002c) reported that up to 95% of hikers had *P. ramorum* on their boots during a four-week study during the rainy season of March 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. Cushman *et al*. (2007) showed that hikers have dispersed *P.*

ramorum in soil on their shoes to a distance of at least 60 to 100 m into areas of a nature reserve in California that lacked local inoculum sources. Mountain bikes were also found to be implicated in the movement of *P. ramorum*. There have been similar findings related to footwear in UK studies. Soil and litter samples were taken from boots prior to disinfection at infested woodlands in south-west England. *Phytophthora* species were present in more than 30% of samples collected from walker's boots. The most commonly occurring species was *Phytophthora citricola*, but 10–15% of the samples contained *P. ramorum* or *Phytophthora kernoviae* (Webber and Rose, 2007).

Additional studies have been done in the US on the extent of dispersal in relation to the movement of people, black-tailed deer, pigs, turkeys, squirrels and jays (H. Cushman, 2004, *personal communication*). In soil samples taken 'on trails' and 'off trails' (areas immediately adjacent to trails) in different habitats, the percentage *P. ramorum* recovery was as follows: grassland adjacent to infected woods, 0% (off-trail) and 45% on trail; Oregon white oak habitat, *ca.* 20% (off trail) and *ca.*100% on trail; and coast live oak-California bay laurel habitat, 100% (on trail) and 100% (off trail). Also, the proportion of symptomatic California bay laurel trees (*U. californica*) was significantly greater in Californian forest plots experiencing high levels of human activity than those with low activity levels (Cushman and Meetenmeyer, 2005). There is therefore evidence for movement associated with trails and human activity. Further research by Cushman and co-workers (2007) has shown that hikers can potentially disperse the pathogen at least 60 to a 100m in soil attached to shoes. Furthermore, if the soil is kept moist, the pathogen could be isolated from shoes up to 72 hours after infested soil is picked up. However, if the shoes were allowed to dry out, *P. ramorum* could not be isolated.

Vertical dispersal of inoculum into the tree canopy has been studied in California in relation to birds (e.g. wild turkeys roosting in trees) and squirrels (J. Arnold and H. Cushman, 2004, *personal communication*).

In nurseries and garden centres it is likely that the pathogen is transmitted through plant to plant contact, splash dispersal, irrigation and the movement of infested debris, soil/growing media and freestanding water or surface water run-off. Therefore, if large blocks of susceptible plants are in close proximity then the pathogen is likely to spread between them through repeated cycles of secondary dispersal. In experiments designed to compare relatively long (1 to 4m) and short distance dispersal (pot to pot) amongst rhododendrons in simulated nursery conditions, new infections were only detected amongst plants within a short distance (adjacent and up to 30cm away) of a centrally-located artificially-infected plant (Tjosvold *et al*., 2005). No infection was detected in the long distance experiments and no inoculum was detected in rain traps located 1 to 4m away from the infected plant during rain events.

Inoculum transfer on pruning equipment has been demonstrated, but no infections developed after using contaminated equipment to prune experimental plants (Defra, 2005c). In a two-year study, the spread of *P. ramorum* with contaminated irrigation water and the survival of the pathogen in water reservoirs were studied (Werres *et al*., 2007b). *Phytophthora*

ramorum was able to survive in the water reservoirs during all seasons and the pathogen could be spread with artificially contaminated water. Disease symptoms on rhododendron were observed in as little as seven days after the first irrigation with contaminated water. However, Tjosvold *et al*. (2005) were unable to successfully infect rhododendron nursery stock using naturally infested stream water in California when irrigated directly onto the surface of the growing media, but this was perhaps due to much lower inoculum levels in naturally infested stream water and the fact that the inoculum was not directly introduced to the leaf surface.

Long distance movement

Goodwin (1997) stated that movement of infected plants or plant parts is probably the most likely avenue for the long distance dispersal of *Phytophthora* species, particularly in woody or fleshy parts that do not dry out easily. This is likely to be the case for *P. ramorum*, where international movement of ornamental nursery plants has resulted in the pathogen being introduced to the USA and Europe from an unknown area or areas. Brown *et al*. (2006b) support the view that plant collectors or the horticultural nursery trade were likely to have been responsible for the introduction of *P. ramorum*. Brasier and Jung (2006) suggest that there is a link between *Phytophthora*-infested nursery stock (referring to the genus *Phytophthora*) and damage to forests with circumstantial evidence of the apparent spread of *P. ramorum* from out-planted rhododendrons or other nursery stock onto *R. ponticum* and then onto trees in Cornwall.

There is good evidence that the nursery trade had a major role in the movement of this pathogen. All three clades of this pathogen (see Table 1) have been identified in some US nurseries (Ivors *et al*., 2006). The ability of nurseries to disperse the pathogen nationwide has also been documented in the USA (Stokstad, 2004), where a nationwide nursery supplier was found to have shipped potentially infected material to 783 garden centres in 39 states over 12 months. There is also anecdotal evidence from northern California that suggests that landscaping with infected horticultural plants in areas adjacent to forestland may have introduced the pathogen to new areas (Davidson and Shaw, 2003).

Slawson *et al*. (2007) reviewed the effects of the EU emergency measures on the number of new findings on nurseries and the number of positive findings on so-called plant-passported material in England and Wales. They found that *P. ramorum* has continued to be found on plant-passported material, albeit at a low level supporting the view that the pathogen is continuing to move in trade. They consider that the results of epidemiological modelling of some of these data (Jeger *et al*., 2007) supports the view that continued action on places of production (nurseries) is warranted. Jeger *et al*. (2007) consider that trace-forward, trace-back information of outbreaks of *P. ramorum* in the UK may enable the reconstruction of the network of pathogen spread which could be useful for informing the management strategy. Pautasso *et al*. (2007) suggest that the properties of the network on which *P. ramorum* is moving in trade is uncertain. However, given that the majority of

positive findings of *P. ramorum* are on rhododendron they suggest that it may be acting as a 'super-connected' susceptible genus; this would be characteristic of what is termed a 'scale-free network'. Scale-free networks have lower epidemiological thresholds than other kinds of networks (local, random, small-world) if the risk of spreading *P. ramorum* from a given nursery to others is correlated to the risk of acquiring the pathogen for that given nursery from other ones, even in the case of a relatively small network size (one hundred individuals) (Pautasso & Jeger, 2008). If this is the type of network on which *P. ramorum* is moving, it increases the potential for spread in trade.

Long distance spread may also occur by the movement of diseased cut bark and wood as logs or sawn wood. Infection has been reported in the xylem (Rizzo *et al*., 2002; Brown and Brasier, 2007) and chlamydospores, which are potentially relatively long lived, have been reported in bark phloem and xylem tissue of some tree species (Parke *et al*., 2007). Preliminary data suggests that *P. ramorum* spores can survive on firewood from susceptible host trees for at least 6 months (Shelly *et al*., 2005). There is a risk that the pathogen could be transferred from firewood stored in the back yard to living hosts, prior to use.

Germination, infection and host susceptibility

Sporangia can germinate in two different ways. At higher temperatures direct germination occurs, this is when the hyphae emerge through the wall of the sporangia. Indirect germination, or zoosporogenesis, occurs at cooler temperatures (below 20ºC) and zoospores are produced within the sporangia. The zoospores are discharged from the sporangium and are motile in water once released. Zoospores then migrate towards host tissue. Eventually the zoospores lose their flagella and form walled cysts that germinate immediately to produce a germ tube that eventually leads to infection. Generally, for *Phytophthora* species, the process of zoosporogenesis, encystment and appressorium formation all occur within a few hours. The duration of this period is unknown for *P. ramorum*.

Plant colonisation via sporangial/zoospore germination occurs through openings such as wounds, or natural openings such as stomata or lenticels. Inoculation studies implicate natural openings such as stomata on leaves or lenticels on shoots as one route of entry (Florance and Parke, 2002). Stomata have been identified as likely sites for the initial infection of camellia (Geltz *et al*., 2005). Wounded tissues also appear to be more susceptible than unwounded tissues. This was demonstrated by Lewis and Parke (2005) using electron microscopy, they observed that hyphae from germinating cysts were attracted to a micro-cavity on a leaf, while none were growing toward a stoma nearby.

Infection by zoospores tends to occur on susceptible plant parts where water accumulates, e.g. leaf tips. Frequency of infection of California bay laurel (*U. californica*) leaves under laboratory conditions was 92% of leaves infected at 18°C, 50% at 12°C and 37% at 30°C (Garbelotto *et al*., 2003); leaves were

infected within 12 hours at 18°C in the presence of free water (D. Huberli, Oregon, 2002, *personal communication*). Garbelotto *et al*. (2003) reported that a minimum of 6 to 12 consecutive hours of free water is a prerequisite for the infection of *U. californica* leaves.

In UK studies (Defra, 2005b), rhododendron leaves were always infected when inoculated on unwounded, lower leaf surfaces where stomata occur; however, under the conditions of these experiments, no infection occurred when unwounded upper leaf surfaces (no stomata) were inoculated. In a separate experiment there was some indication that wounds may be more important for infection of some hosts than others: leaves of some hosts were infected without wounding even with low levels of zoospore inoculum (1,000 zoospores/ml), e.g. *R. ponticum*, *R. catawbiense* and *F. excelsior*; others were only infected when leaves were wounded, even with high levels of inoculum (100,000 zoospores/ml), e.g. *Camellia japonica*. Data also suggests that leaves of different hosts have different inoculum thresholds.

Infection of mature tree bark has been demonstrated experimentally for several hosts in the absence of wounds (Webber, 2004). *Phytophthora ramorum* can penetrate bark without the need for wounding or natural openings, for example, zoospores have been shown to be able to penetrate beech (*F. sylvatica*) bark (Brown *et al*., 2005). Saplings of many tree hosts are less susceptible (or resistant) to direct bark infection than mature bark. In studies in the UK, saplings of various species were only infected when wounded, trees were also more susceptible in the summer than in the winter (Defra, 2005c). In experiments designed to assess the capacity of *P. ramorum* zoospores to infect the phloem tissue through intact bark of several tree species, infection and developing necrosis occurred after two weeks in the absence of any wound (Webber, 2004).

Swiecki & Bernhardt (2006) showed that for coast live oak (*Q. agrifolia*), bark thickness and unweathered brown tissue within bark fissures were positively correlated with *P. ramorum* disease risk. These areas of tissue may represent relatively rapidly expanding regions of the outer bark in fast-growing trees. Bark expansion zones may be more easily breached by *P. ramorum* zoospores. The outer periderm in these areas may be so thin that plant substances can diffuse from them when the bark surface is wet, which may attract *P. ramorum* zoospores. If this does occur, and it is not yet proven, a high aggregation of zoospores cysts may develop increasing the chance of infection. Bark fissures may be wetter longer than other areas of the bark which would also favour infection.

Once within the bark, the pathogen spreads within the phloem and cambial tissues and may also progress to a limited degree into the outer sapwood. Infection and discolouration, is more extensive in cambium and secondary phloem tissues than in the xylem, however, infection has been reported in the xylem (Rizzo et al., 2002; Brown and Brasier, 2007; Parke *et al*. 2007). Florance (2002) showed that both lenticels and stomata can serve as points of entry for the hyphae of *P. ramorum* through microscopic examination of stem and leaf tissue samples of *U. californica*, *Quercus* spp. and *R.*

macrophyllum naturally infected with *P. ramorum*. Hyphae were also observed growing in the vascular tissues of the stem.

It has been suggested that *P. ramorum* can move within plants and trees through the vascular tissues (xylem) in addition to other tissues. Cankers up to 20 m from the base of *Quercus* species and *L. densiflorus* trees have been found (Rizzo *et al*., 2002) and movement of spores or mycelium within the xylem could explain this although it is not yet proven (Brown & Brasier, 2007). Parke *et al*. (2007) postulated that the presence of *P. ramorum* in the xylem vessels could contribute to 'sudden oak death' syndrome; they observed that sap flow and specific conductivity were significantly reduced in infected trees.

A histological study with rhododendron twigs (Pogoda and Werres, 2004) showed that *P. ramorum* could colonise different tissues. Hyphae were found in all tissues of the necrotic zone: the cortex, phloem, xylem and pith. Hyphae were also present in the cortex and pith of healthy looking material about 1 cm below visible traces of discolouration whereas chlamydospores were only observed in the necrotic zone where they developed mainly in the cortical parenchyma. This study also showed that *P. ramorum* can grow both intra- and intercellularly but chlamydospores were only observed in the intercellular spaces. In similar studies on rhododendron leaves and roots (Riedel *et al*., 2007) hyphae were again located in the cortex and pith where discolouration was present. In healthy looking stems and roots hyphae were usually found in secondary xylem tissue.

Inoculum pressure is likely to play a major role in determining whether disease develops or not. Damage to tree trunks and subsequent death of susceptible tree species might only occur if they are subjected to high inoculum pressure from spores produced on nearby infected foliar hosts. Tree hosts that may be susceptible to trunk infections, which do not produce sporangia on their foliage do not provide their own inoculum. Trees that display only bleeding cankers are commonly referred to as terminal tree hosts.

Differences in susceptibility under varying inoculum pressure has been observed for ornamental and under-storey hosts (Defra, 2005b). For example, at low inoculum pressures (1.3×10^3 zoospores/ml), *Sambucus nigra* (common elder), *S. vulgaris* (lilac), *U. californica* (California bay laurel) and *Lonicera periclymenum* (honeysuckle) were not infected in detached leaf assays with unwounded leaves. However, when the amount of inoculum pressure was increased (2.3×10^5 zoospores/ml), 67 to 100% of the leaves inoculated became infected. Wounding also had an influence on whether disease developed or not, for example, unwounded leaves of *C. japonica* remained uninfected at both low and high inoculum pressures, but 33% of wounded leaves were infected at the low inoculum pressure and 100% at the high inoculum pressure.

Incubation period and latency

In experiments in the UK (Defra, 2005c), the time period between infection and appearance of symptoms on rhododendron leaves decreased with increasing temperature. Largest lesions were produced after incubation at 25°C with over 75% of the leaf area affected after 12 days compared with less than 2% leaf area affected after incubation at 0°C. There was evidence of a positive relationship between accumulated temperature and lesion development (up to 25°C). No evidence was found for truly latent infection, with symptoms appearing after three days under optimum conditions. Symptoms appeared within 14 days of initial infection even at 0°C.

More data on latency in magnolia buds are being generated from studied undertaken by Forest Research (pending publication).

Survival

The pathogen may survive over short or long periods of time depending on environmental conditions (substrate, abiotic factors) and spore type. The pathogen has the potential to survive in various substrates, e.g. soil/growing media, water, leaf debris, within infected plant material or for short periods on inert surfaces. This section summarises the literature with regards to the survival of *P. ramorum*.

Survival of pathogen structures in laboratory tests

Laboratory studies in the UK (Defra, 2005c) have shown that sporangia and chlamydospores were able to survive and germinate on agar after exposure to -2 °C for 24 hours . Chlamydospores were not capable of germinating after exposure to 55 °C for one hour. No chlamydospores germinated following exposure to 40 °C for 24 hours or –25 °C for just 4 hours. No sporangia survived a 2-hour exposure to these temperatures. Sporangia were found to survive up to 6 hours but not 24 hours at room temperature in moisture-free conditions. Sporangia were able to survive short exposures (experiments only tested exposures up to 6 hours) to pH regimes in the range of pH 3 to pH 9, but did not survive at pH 2 for 6 hours.

Further UK *in vitro* work has been completed on chlamydospore survival after exposure to different temperatures under laboratory conditions (Turner and Jennings, 2006). Chlamydospores were incubated at –25, 0, 5, 15, 30 and 40°C. Chlamydospores survived at all temperatures except at –25°C and 40°C for up to two months.

Laboratory studies in the USA showed that chlamydospores were apparently killed in culture when exposed to 55°C for 1 hour, confirming the UK data, or 2 hours at 45°C or 24 hours at 40°C (Swain *et al*., 2006). In a study by Davidson *et al*. (2002a) chlamydospores of *P. ramorum* survived relatively well in de-ionised water, with 75% still viable after 30 days whilst less than 20% zoospores remained viable. On moist filter paper 41% of chlamydospores germinated whilst less than 20% of zoospores remained viable. Zoospores and chlamydospores were unable to survive on dry filter

paper but sporangia were shown to survive up to 6 hours, whilst none survived after 24 hours. Zoospores/zoospore cysts have been shown experimentally to survive in distilled water at 15ºC for approximately 200 days whereas chlamydospores survived in distilled water at 15ºC for 350 days (J. Davidson, 2003, *personal communication*).

In another study in the USA (Tooley and Browning, 2007), chlamydospores were incubated in sand at temperatures ranging from –20ºC to 40ºC. After seven days, near 100% survival was observed at 0ºC and 20 ºC, whilst no survival was observed at –10ºC or –20ºC over the same period. For the higher temperature treatments, high levels of chlamydospore germination were observed over the 7-day period at 30ºC and 20ºC, whilst no growth occurred at 40ºC. At 35ºC, high levels of chlamydospore germination were initially observed, but this declined steadily until there was no germination after 7 days.

Survival in plant material

Phytophthora ramorum can survive outdoors in plant material for longer periods than tested in studies under laboratory conditions mentioned above. In the UK, the pathogen can survive as infections on plants. This can be active infections on evergreen hosts such as rhododendron (Defra, 2007d) or as quiescent infections in buds (e.g. on deciduous magnolia species (J. Webber, Forest Research, *personal communication*). In the USA (California), the pathogen primarily survives over the hot dry summer as infections on evergreen leaves (Davidson *et al*., 2002a).

Experiments investigating the over wintering of *P. ramorum* in leaf debris were undertaken in the UK between November 2003 and March 2004 (Defra, 2005c). In this experiment the pathogen survived in leaf tissue of rhododendron and lilac (*S. vulgaris*), both on the soil surface and buried 5cm below the soil surface, under UK conditions outside under containment. Pathogen survival under ambient conditions during the winter of 2003/04 gradually decreased over time, but the pathogen could be recovered from at least 50% of leaves in all treatments (host leaf/burial depth). The winter was relatively mild with night temperatures reaching a minimum of –9°C. Survival was slightly higher on the evergreen host (rhododendron) compared to the deciduous host (lilac); the leaf tissue of the latter degenerated over the period of the experiment. Survival was highest on rhododendron leaves that had been buried 5 cm below the soil surface, with over 80% of leaves still yielding the pathogen after four months. Tests carried out in Scotland in a parallel experiment also showed similar survival under ambient conditions over the same period; the pathogen could also be recovered after a second winter. These UK over-wintering experiments therefore showed survival over the winter in both lilac and rhododendron leaf material as either surface leaf litter or buried in soil at sites in northern England and Scotland.

In leaf-debris survival experiments in Oregon, the pathogen survived better in buried *Rhododendron* and *L. densiflorus* (tanoak) leaves after 8 weeks (89% leaves positive) than those on the soil surface in shade (66% recovery) or on

the soil surface exposed to the sun (26% recovery) (McLaughlin *et al*., 2006). In another study, *Rhododendron* leaf tissue containing chlamydospores was buried in mesh bags in pots containing nursery stock and incubated in a greenhouse, the pathogen could be isolated for up to 155 days after burial (Shishkoff and Tooley, 2004).

The main means of survival over summer in California appears to be as infections in evergreen California bay laurel (*U. californica*) leaves. Davidson *et al*., 2002a found that survival in attached leaves declined from 90% in June to 50% in August 2002, compared to virtually zero in abscised leaves over the same period. Leaves that were infected by the end of the first census period (April – first marked in January) were 15 times more likely to abscise than uninfected leaves by the end of the second census period (July 2002). It was surmised that over-summering in attached California bay laurel leaves is most likely to be facilitated by two main factors: chlamydospores form prolifically in lesions on this host, leaf necrosis is limited (lesions are mostly restricted to the leaf tip or margin) and therefore are not killed or abscised quickly.

At eradication sites in Oregon, the pathogen can also survive in tanoak (*L. densiflorus*) stumps and infected re-growth from cut stumps (Hansen and Sutton, 2005). At eradication sites in the UK, the pathogen has been observed on new shoots emerging from the stumps of cut rhododendron (Defra, 2007d).

Preliminary data suggests that *P. ramorum* spores can survive on firewood from susceptible host trees for at least 6 months (Shelly *et al*., 2005).

Survival in water, soil and potting media

In the UK, *P. ramorum* has been shown to survive for considerable periods in the absence of the host. *P. ramorum* was detected in soil for almost two years after the removal of infected rhododendron at a site in Cornwall (Lockley *et al*., 2007). In the Netherlands, it was demonstrated that the pathogen remained viable for at least one year in sandy soil (Aveskamp *et al*., 2005). *P. ramorum* has also been found at depths of up to 15 cm in soil in areas of severe plant infection (Turner *et al*., 2007). Monitoring at other sites where eradication action was taken early in the disease epidemic has shown that, in the absence of inoculum sources, residual contamination in soil will decline slowly over time and in some cases this will decline below thresholds of detection (J. Turner, *personal communication*)

In the USA, Linderman and Davis (2006) found that *P. ramorum* could survive in potting media or soil for up to six months when the pathogen was introduced to the media as sporangia and for up to 12 months when introduced as chlamydospores. A four-month study found no decline in chlamydospore populations in sand, potting soil mix and forest soil stored at 4°C (Colburn *et al*., 2005). However, a small decline in the number of chlamydospores was observed at 22°C and chlamydospore survival was lowest in forest soils, suggesting that some of the biologically active components of forest soil may be active against chlamydospores. In

experiments with potting mix, *P. ramorum* was recovered after storage for up to 12 weeks at 4°C but not from a sample stored at room temperature for 10 weeks (Jeffers, 2005).

Fichtner *et al*. (2005) found that *P. ramorum* survived well in the soil and litter/soil interface (recovery from infected rhododendron leaf discs 80% and 60% respectively after 8 weeks) in redwood-tanoak forests. The pathogen survived poorly on the leaf litter surface (only 1% recovery from leaf discs after a week). *P. ramorum* was recovered from 60% of the leaf discs incubated in forest soil for six months. Soil moisture was shown to correlate with pathogen recovery.

In wild environments in California, the pathogen has been isolated from the soil during the rainy season (Davidson *et al*., 2002a; Maloney *et al*., 2002), but not from soil or debris during the hot, dry summer months (June–December). The pathogen is also recoverable from water courses during the rainy season (Davidson *et al*., 2002a; Maloney *et al*., 2002); although one study (Davidson *et al*., 2002a) did not detect the pathogen in water samples taken from streams in the summer, another study using baits placed into streams did recover the pathogen during the summer, irrespective of rain events (Maloney *et al*., 2002).

Seasonal variation of inoculum levels in watercourses (streams and ponds) has also been observed in the UK (Turner *et al*., 2007). The highest levels of inoculum as detected by bait tests occurred in winter and spring and lower levels in the summer. Inoculum at one site in south-east England persisted in a stream over a period of three years post-eradication of the outbreak. However, levels did decline over time and no new plant infections occurred during the monitoring.

Survival of oospores

Oospores of *P. ramorum* have not been reported in the field in either North America or Europe. The oospores of *Phytophthora* species are typically thick-walled and durable sexually-produced spores that typically remain viable between growing seasons. They are often an important source of inoculum, particularly for homothallic species and for heterothallic species where both mating types share the same geographical area (Judelson and Blanco, 2005). *Phytophthora ramorum* is a heterothallic species, and the mating types are geographically separated in the main with a few findings of opposite mating types on nurseries in Belgium as well as in North America. Werres *et al*. (2007a) found in studies of the result of pairings of A1 and A2 isolates of *P. ramorum* that 9 to 77% (average *ca*. 30%) of the *P. ramorum* gametangia of the 900 they assessed contained apparently viable (tested using a vital stain) but often thin-walled oospores. However, *ca*. 94–97% of the gametangia of the homothallic species they assessed (*P. kernoviae* and *P. citricola*) produced thick-walled oospores, as did 55% of the heterothallic species *P. cambivora*. The authors suggested that the thin-walled oospores of *P. ramorum* could be more susceptible to biodegradation than the thick-walled oospores of many other *Phytophthora* species. They suggested that there

may be a different dispersal/survival strategy for *P. ramorum* to other *Phytophthora* species such as more rapid germination on plant surfaces or a greater potential to germinate after ingestion by arthropods or molluscs; for *P. ramorum*, oospores may not be a principal long-term survival structure (if they can be produced), a role that is currently served by chlamydospores. Results may reflect the experimental conditions under which the work was undertaken.

The discovery of three A2 isolates of *P. ramorum* in Belgium (K. Heungens, *personal communication*) and the production of oospores under laboratory conditions in some pairings investigated in Belgium and studies at CSL (P. Giltrap, *personal communication*) the viability of which was unproven suggests oospore survival should still be considered. However, Werres *et al*. (2007a) reported that pairings between EU1 (A1) and one Belgium EU1 (A2) isolate failed to result in oogonia or oospores being formed. Further research is required to determine the potential role of oospores in the long-term survival and epidemiology of *P. ramorum.*

Factors affecting disease development

Factors affecting disease development and severity are discussed in general terms here: these factors include abiotic/climatic factors (e.g. temperature and moisture) and biotic factors (host susceptibility and host associations).

Phytophthora ramorum has an optimum growth temperature of 20°C (Werres *et al.,* 2001). The temperature determines whether the sporangia germinate directly or produce zoospores. Moisture is essential for sporangial detachment and zoospore motility. Cool moist conditions are therefore most likely to favour disease development and spread. Risk mapping approaches using climate data can be used to predict areas most likely to be at risk from *P. ramorum* (e.g. Venette & Cohen, 2006); Magarey *et al*., 2007). Such risk mapping can also take account of biotic factors such as host distribution and host associations. (e.g. Baker, 2007; Meentemeyer *et al*., 2004; Kluja *et al*., 2007).

Laboratory-determined optimum conditions for the pathogen might not be the same in the natural environment where many factors will interact to influence disease development. Condenso and Meentemeyer (2007) made observations of plots of infected forest trees in northern California, high disease severity was associated with lower temperatures in the field (0–10°C) than for the optimal range for zoospore production (15–20 °C) determined under laboratory conditions by Davidson *et al.* (2005). They speculate that in the field, temperature and relative humidity may affect the susceptibility of California bay laurel (*U. californica*), with lower temperatures and moist conditions causing the leaf stomata to be open for longer periods thus allowing more opportunity for infection to occur. Water is likely to remain on the leaves for longer at lower temperatures.

In the USA, analysis of a number of variables suggests that bole cankers (bark necrosis) of coast live oak (*Q. agrifolia*) caused by *P. ramorum* is more

likely to occur in trees that are vigorous and/or fast growing (i.e. trees that are larger, more dominant, less water stressed and not in decline due to other agents) than in trees that are suppressed and/or slow growing. Tree factors correlated with disease were: multiple stems, large stem cross-sectional area, high levels of canopy exposure and stem water potential; other factors that correlated with disease included the count of California bay laurel (*U. californica*) trees. *Q. agrifolia* (Coast live oak) trees at drier sites in California appear to be at a lower risk for disease than those in damper sites (Swiecki and Bernhardt, 2002, 2003). Rizzo *et al*., 2005 reviewed this and later work and suggested that based upon experiments on a limited number of tanoak trees (*L. densiflorus*), a significant positive correlation between stem water potential and disease has been found suggesting that tree disease is not more common on water-stressed trees and that water stress may not be as important a predisposition factor as it is with other plant diseases.

Condenso and Meetenmeyer (2007) found a positive association between disease severity and elevation in Californian forests. They attributed this to topographically driven differences in optimal temperature and moisture conditions for *P. ramorum*. However, they suggest that it is also possible that greater wind velocities at high elevations increase the rate of leaf-to-leaf and or tree-to-tree spread.

There are topographical factors associated with outbreaks in the UK with a number of outbreaks being located in coastal valleys, near to watercourses, and associated with pathways etc.

SOCIOECONOMIC AND ENVIRONMENTAL IMPACTS

Environmental and commercial impacts in forests and woodlands and potential impacts for heathlands

In Europe, few trees have been affected and these have only been recorded in the Netherlands and the UK, with the first being detected in October 2003 in both countries. According to the RAPRA EU Project database (interrogated 11th July 2007) the numbers of trees affected in the Netherlands are currently six beeches (*F. sylvatica*) and eight northern red oaks (*Q. rubra*). As of February 2007, 82 trees are known to have been infected with *P. ramorum* in the UK: these include foliar infections on 62 individual trees and stem cankers on 20 trees; 13 of these trees have been felled as part of the eradication activities (J. Webber, *personal communication*).

Turner *et al*. (2007) reported that between October 2003 and February 2007 there were 160 outbreaks of *P. ramorum* in the UK in locations other than nurseries (i.e. in gardens or woodlands). Of these, 123 were still ongoing in February 2007 and the rest were considered eradicated. Eradication is considered to have been achieved where there have been no further plant infections; however, *P. ramorum* was still present in soil and water at some of these sites. Updated figures (D. Slawson, *personal communication*) show that between April 2002 and June 2007 there have been 185 outbreaks at 166 sites in locations other than nurseries of which 60 have been eradicated.

In the USA, the major impact of *P. ramorum* to date has been on the coastal woodland environment of California. Symptoms of *P. ramorum* were first reported on trees there in the mid-1990s. Since then, it is estimated that over a million oak trees have been killed, including. *L. densiflorus* (tanoak), *Q. agrifolia* (coast live oak) and *Q. kelloggii* (Californian black oak) (Shoemaker *et al*., 2007). Other species of woodland plants have suffered non-lethal foliar and shoot infections. Woodland in Oregon has also become affected. Several US and Canadian nurseries were first reported affected in 2003 with a substantial increase in findings across the USA in 2004 related to movement of infected plant material from a large wholesale nursery in California (Suslow, 2005).

The most visible impact of *P. ramorum* has been in the USA with the death of over a million tanoak and true oak species in Californian forests. Rizzo *et al*. (2005) reviewed the pathogen and described the occurrence of *P. ramorum* in the coastal forests that have been affected in California and Oregon as 'patchy'. At the time of writing (2005), at the largest scale the incidence of the pathogen was described as discontinuous in coastal forests from the Big Sur (Monterey County) into central California and on to Curry County, Oregon; a distance of 750km. Most forest sites affected were within 30km of the Pacific Coast or San Francisco Bay, along a distance of *ca*. 450km. Areas within the affected areas that were free of disease often contained susceptible hosts and the authors speculated that the absence of disease there is historical (i.e. not yet introduced) rather than related to the environment, or the biology of *P. ramorum*. Because the pathogen is not subject to eradication in California it still has the potential to affect trees and shrubs in unaffected areas, provided a sporulating host such as California bay laurel (*U. californica*) or tanoak (*L. densiflorus*) is present. Rizzo *et al*. (2005) state that because many of the tree species (presumably in the USA) are not commercially important, the economic effects of biotic agents including *P. ramorum* have not been characterised. However, research plots have been established in various forest locations and impacts have been assessed experimentally. Mortality of tanoak (*L. densiflorus*) and coast live oak (*Q. agrifolia*) has been found to be increased by the presence of *P. ramorum* compared to either baseline mortality or other factors, including other diseases. The loss of oaks (*Quercus* spp.) and tanoak (*L. densiflorus*) in California has changed the forest stand structures. It is likely that those plant or tree species that are less susceptible or not susceptible will thrive and increase their population thus changing the local ecology. No data have yet been gathered on the long-term impacts as it is still relatively early in the course of the epidemic.

Klieujunas (2003) suggested that in North America, heavy loss of oaks, or of related susceptible genera, due to *P. ramorum* infection could result in significant ecological effects, including changes in forest composition, loss of wildlife food and habitat, increased soil erosion and a significant increase in fuel loads for forest fires in heavily populated urban-forest interfaces. *Quercus* spp. are considered the most important and widespread of the hardwood trees in the 'North Temperate Zone', with about 300 species. Oaks are widespread across North America and Eurasia, extending south in tropical mountains to Cuba, Colombia, northern Africa, and Indonesia. In California,

oak woodlands yield important benefits, including water and watershed protection, grazing, wildlife food and habitat, recreation, and wood products.

Kliejunas (2003) also states that many of the foliar hosts of *P. ramorum* have ecological significance. *Rhododendron* spp. occur worldwide, and some species in the United States are currently listed under the Endangered Species Act. *Vaccinium ovatum* (evergreen huckleberry), native to British Columbia, Washington, Oregon and California, is a common understory component of California and Oregon forests. *Vaccinium* spp. are widely distributed throughout Europe, Asia, and North America; more than 40 species occur in North America.

In addition to the suggested potential environmental impacts due to disruption to the ecology of the area described above, Appiah *et al*. (2004) include a loss of recreational areas in woodland severely infested with *P. ramorum*, with the presence of dead trees increasing the risk of accelerated water run off, and, as alluded to by Klieujunas (2003), resultant soil erosion and sedimentation and endangering of certain plant species. There is a particular risk from forest fires because of the presence of dead trees and also the risk to power lines. Two small (less than 1 hectare) fires (one in Napa County and one in Sonoma County) have been caused by SOD-killed trees snapping and hitting powerlines. The Northern California utility company, Pacific Gas and Electric Company, has accelerated clearing along lines to prevent hazards. (Susan Frankel *personal communication*). Local landowners in the infested areas in coastal California have had to pay for the clearance of dead trees to protect homes and property.

There have been several studies showing how *P. ramorum* mediated tree death can affect forest wildlife. These have been mainly done in California. These studies have shown that *P. ramorum* can lead to changes in vegetation structure. Oaks may become less dominant and California bay laurel (*U. californica*) becomes more prevalent. This can lead to an open canopy and ultimately, increased light levels could result in dense shrub cover (Winslow and Tietje, 2005). This may affect bird communities with the loss of prey habitat and nesting sites. This theory is concordant with Apigian and Allen-Diaz (2005) who observed a loss of bird nest sites, prey reduction and loss of foraging substrates in *P. ramorum* affected plots. Projections on the effects of *P. ramorum* on bird populations associated with *Q. agrifolia* in California have indicated that the bird population could be 25–68% smaller and 13–49% more variable relative to estimates prior to infection with *P. ramorum* (Monahan and Koenig, 2006).

Effects on other animals are evident. It has been shown that an infected tree can attract greater numbers of beetles (McPherson *et al*., 2005). This may also affect the feeding patterns of birds. Some small mammal species may benefit from loss of trees due to *P. ramorum*. In California, wood rats were projected to benefit from the increased shrub cover, California mice would benefit from an increase in coarse wood debris and brush mice would benefit from lower tree densities. Two salamander species modelled were likely to be relatively unaffected. (Tempel and Tietje, 2005).

Environmental impacts of invasive species in general are difficult to put into a quantitative context because of the non-market value of the resources, and to date there are few cases where economic values have been placed on such invasions (Waage *et al*., 2006). However, it has been postulated that the cost of environmentally invasive species (which *P. ramorum* can be classed as) rises with time. This is because they can be relatively slow spreading compared to crop diseases, and need to reach very high densities before they cause losses (in terms of biodiversity or ecosystem services); also, future wealthier societies are likely to place a greater value on the environment (Waage *et al*., 2006).

Widespread tree death can result in direct economic loss if timber plantations become affected, however, this has not occurred in the UK, EU, US or Canada and so it has not been costed. Timber species in California are not thought to be at risk of mortality from *P. ramorum* (Rizzo *et al*., 2005). However, in terms of direct economic impact, hardwood tree species in coastal California have historically been treated as "weeds" but now a hardwood timber products industry is developing there. In 2002, the state's oak woodlands were estimated to contain about 5 billion cubic feet of wood valued at over $275 million. The 5.8 billion cubic feet of oaks in nearby California timberlands were worth over $500 million for forest products alone. It was estimated that if oaks and other tree species in the eastern deciduous forests of the USA became affected by the pathogen, the potential cost to commercial timber production in the United States was likely to be in excess of $30 billion. (Klieujunas, 2002). Cave *et al*. (2005) referred to the value of the US cut Christmas tree industry in 2003 as $520 million. One of the major Christmas tree species, *Pseudotsuga menziesii* (Douglas fir), is recorded as a natural dieback host of *P. ramorum* in the USA; Oregon is the US state that produces the greatest number of these trees for the Christmas trade (USDA, 2005).

In the UK, woodlands/forests provide a variety of benefits including open-access free recreation, landscape amenity, biodiversity and carbon sequestration. Forests also impact on water supply and quality, pollution absorption, health effects and the preservation of archaeological artefacts. A study to assign values to these benefits is summarised in Appendix 4. This estimated that the social and environmental benefits of British forests are *ca*. £1022 million per year (2003 figures). This figure was based on estimated values of the recreational and biodiversity benefits, landscape value and carbon sequestration. The estimated annual value of timber is small in comparison to this (*ca*. £36m (2003 figures)) but there are obvious benefits in employment related to this raw material as well as the products produced from it. An estimated value of British forests can therefore be made from both the values of raw timber and the social and environmental benefits. This is *ca.* £1058 million per year (2003 figures).

Phytophthora ramorum has the potential to affect heathland environments. Experiments determining the susceptibility of heathland hosts (Defra, 2005b) found that bilberry (*Vaccinium myrtillus*) and heather (*Calluna vulgaris*) were most susceptible and also had the potential to support a high amount of

sporulation. *Phytophthora ramorum* is yet to be found in a heathland environment in the UK despite official surveillance; should this occur the pathogen has the potential to affect key plant species with consequences for the ecology of this important habitat.

Impacts on nurseries

Outbreaks of *P. ramorum* on nurseries and retail premises have been found in fifteen EU Member States with *P. ramorum* being detected on 14 plant genera. Currently 99 nursery outbreaks are subject to phytosanitary measures in England and Wales with 459 having been eradicated between April 2002 and June 2007 (D. Slawson, *personal communication*). In England and Wales, 96% of nursery findings have been made on *Rhododendron*, *Viburnum* and *Camellia* – the three genera that are subject to the Plant Passporting regime for *P. ramorum* in the EU (Slawson *et al*., 2007). In Scotland, between 2002 and up to June 2007 there have been 34 nursery outbreaks of which 32 were eradicated by 2005, with none occurring in 2006, and 2 new outbreaks in 2007. A provisional figure for the value of hardy ornamental nursery stock produced in the UK for 2005 is £781,359,000 (Defra, 2006a), but no specific figures are available for the value of individual genera that have been affected, nor for the losses associated with *P. ramorum* other than the costs of implementing the emergency phytosanitary measures (see below).

In the USA, figures are again not available for the direct impacts on nurseries other than those resulting from the phytosanitary measures. Klieujunas (2003) reported that during 1997, about 14.2 million potted florist azaleas (*Rhododendron* spp.) valued at $48.3 million were produced in the United States. This figure does not include nursery azalea and rhododendron production. Some other foliar hosts are also economically significant. The foliage of *Vaccinium ovatum*, (evergreen huckleberry), a natural host in the USA which is browsed by elk, is also harvested for use in floral arrangements. In the 1970s, an estimated $1 million worth of foliage was harvested annually in western Washington. The genus also includes the commercially important blueberries and cranberries. Cave *et al*. (2005) reported that in 2003 the US production of nursery stock was valued at approximately $9.2 billion. The USDA (2005) reported that the US ornamental nursery industry was valued at $13 billion with California and Oregon being the first and fifth most important producer of ornamentals.

Impacts on managed gardens

Established parks and gardens are affected by outbreaks of *P. ramorum* in a range of UK locations but especially in the south-west of England (Wright, 2007). Significantly in late October 2007 a single beech tree (*F. sylvatica*) was found at a managed garden site in West Yorkshire co-located with infected *R. ponticum* (D. Slawson, *personal communication*). The visual effect of the pathogen on shrubs and trees in these gardens and the costs associated with their removal and for replacement planting has not been calculated. A study of the numbers of visitors to the affected gardens over

time may indicate the effect on tourism, but these figures have not been obtained as they are not immediately available. There is also a direct threat to heritage trees and plants, and potential for impacts on National Plant Collections, should the pathogen be introduced.

Costs and benefits of phytosanitary measures

A full cost benefit analysis of the emergency phytosanitary measures that have been implemented against *P. ramorum* in the UK, EU and North America has not been feasible. The main difficulty is the absence of data on the economic, environmental and social effects of the pathogen itself in the absence of measures on commercial premises (propagators, wholesale and retail nurseries and garden centres), managed gardens and tourism, and, woodlands or forests.

From a management perspective, UK studies have shown (Defra 2007d) that the benefit arising from removal of rhododendron in woodlands where trees have developed stem cankers, is that this has prevented the development of new cankers on the remaining trees within the woods.

With respect to costs associated with management of the disease in outdoor locations in the UK, based upon work in Cornwall, the costs of clearance for *R. ponticum* (as a control strategy for both *P. ramorum* and *Phytophthora kernoviae*) are estimated at £7,000 per ha for woodland and £10,000 per ha for public gardens (I. Sanders, PHSI, *personal communication*, 2007). Eradication in Oregon through the removal and destruction of infected plants and the treatment of regrowth with herbicide has restricted the disease to a small area near the town of Brookings; these efforts are likely to be protracted however (Kanaskie *et al*., 2007). In California there is no attempt at eradication as the disease has spread to an area which is too large to manage in this way.

The costs associated with the phytosanitary measures in both the EU and North America are available in broad-terms with a little more detail in some reports. These are given below.

Kehlenbeck (2007) estimated the current and future economic and environmental impact of *P. ramorum* in three systems/scenarios in Europe. For the 'nursery system' the impact is currently moderate and includes the costs of implementing phytosanitary measures and the resultant effects on trade. This is not likely to change much if the existing measures are maintained. In the 'northern European tree system' (trees with stem cankers in association with infected rhododendron in the Netherlands and the UK) the impact is also moderate and is related to the environmental impact being limited to a few areas only. This is also not likely to change unless there is a dramatic change in the presence of infected foliar hosts that sporulate sufficiently to provide inoculum to infect tree stem hosts. In the 'southern European tree system', a hypothetical system based upon the presence of the infected foliar host *Q. ilex* (holm oak), currently the impacts are minimal as *P. ramorum* has not been detected there in the natural environment.

However, should the pathogen be introduced, the impact would shift to major because the environment is considered to be highly favourable to the establishment of *P. ramorum*. UK data (excluding Forestry Commission and Forest Research) provided by CSL and Defra (Plant Health and Seeds Inspectorate (PHSI) and Plant Health Division) to support Kehlenbeck (2007) showed that the average costs per annum (2004 to 2006) expended on official inspections were €972, 000 for nurseries and €3,500,000 for parks, gardens and woodlands (January 2007 exchange rates). Costs of additional PHSI staff amounted to €70,000 per annum with costs of CSL research, diagnosis and consultancy advice costing €533,326, €348,100 and €167,979 per annum respectively. Estimates of costs to nurseries were also made, with the costs of Plant Passports being broadly-classified as 'low', hygiene measures and trade effects 'medium' and treatments at major outbreak sites being 'high'. Cost-benefit analysis of all of these factors is yet to be undertaken.

Dart & Chastagner (2007) estimated the losses for Washington State nurseries due to plant destruction as part of the requisite phytosanitary measures for 2004 and 2005. They calculated that 17,266 plants were destroyed at 32 nurseries with an estimated retail value of $423,043. The most commonly destroyed genera were *Rhododendron* (89%), *Calluna* (4%) and *Camellia* (4%). No information was obtainable on the costs of any of the other aspects of the phytosanitary measures, including restrictions on trade resulting from a 90 day holding period for plants that are not destroyed, or on the direct effect on the nurseries themselves. However, one nursery reported that in addition to the value of 109 plants destroyed (1% of total retail value for losses for Washington State) they spent $30,000 on labour, fees for plant disposal and other risk management measures. The conclusion was that the economic impacts on affected nurseries in Washington were greater than the value of the plants that have been destroyed.

Allen *et al*. (2003) evaluated the impact of the introduction of import restrictions in Canada along with surveys and related activities prior to the first findings of *P. ramorum* on nurseries as approximately $1 million (Canadian dollars). This included loss of access to propagation and planting material from California, such as strawberry plants with soil, rhododendrons and indoor palms. The conclusion was that the necessary precautionary approach taken by Canada before the pathogen was detected there resulted in a substantial economic impact; it was anticipated that the regulations might be relaxed as new information came to light which would reduce the impact on trade whilst offering the necessary phytosanitary protection.

The USDA (2005) estimated that regulatory actions had the potential to affect the redwood and Douglas fir industry in California up to a cost of $50 million. Large sums of money have been expended by the agencies, state departments and privately . These are estimated by year as: 2000 - $220,000; 2001 - $8,376,000; 2002 - $3,973,000; 2004 - $26,234,000 and 2005 - $20, 815, 000.

Summary of economic impacts

Currently *P. ramorum* is subject to phytosanitary measures in the areas of the EU/UK where it occurs, so its full impact, in the absence of statutory control, remains unknown. Clearly the pathogen has caused massive (but uncosted) damage to trees and other woodland species in California and to a lesser extent in Oregon. This has not happened to such an extent in the EU with locally damaging outbreaks on trees in woodlands occurring only in the UK and the Netherlands , and outbreaks in managed gardens only in the UK . The pathogen is now relatively widely distributed, but at low incidence in the EU nursery industry but the phytosanitary measures that are in place are reducing the number of new outbreaks in the EU and in England and Wales where for the latter, the number of new outbreaks fell from 161 in 2003 to 34 in 2006 (Slawson *et al*., 2007). The costs associated with the phytosanitary measures, particularly for outbreaks in semi-natural or natural environments, are large but they are still a relatively small proportion of the value of the forestry and ornamental trades in the UK and the USA/Canada. Nonetheless the direct effect of *P. ramorum* has not been costed, even in California, and so no cost-benefit analysis of the measures has been undertaken.

CONTROL

This section discusses the control options that would be available should the pathogen become endemic and deregulated. Strategies for eradication and to reduce the risk of introduction are discussed in the section on 'Phytosanitary measures', though there is clearly some potential overlap between the sections.

Chemical methods

A range of chemicals are available that have activity against *Phytophthora* species. These could be applied to plants and trees in nursery and to some extent, woodland settings and managed gardens. These include chemicals with protective and/or curative activity. Work determining the effectiveness of chemical control has been done *in vitro*, on detached leaves and shoots, and also on whole plants. A description of the work on chemical control described in each of these categories is given below.

According to the UK Pesticide Guide (Whitehead, 2006) the following fungicides are registered for use against *Phytophthora* diseases on ornamental nursery stock in the UK: etridiazole, fosetyl-aluminium, metalaxyl-M and propamocarb hydrochloride. However, more chemicals are currently available under the long-term extension of use arrangements. Please note that metalaxyl-M is also known as mefonoxam in the USA; both names are used below depending upon the origin of the original research.

Effectiveness of chemicals as tested in vitro

In the following paragraphs, studies conducted in the absence of the host plant are referred to as *in vitro*. These studies usually refer to where the pathogen is grown in media (usually agar based) amended with various concentrations of a chemical. This method determines the effect any given

chemical can have on hyphal growth. However, the activity of some chemicals is also expressed as the effect on spore germination which is measured using photometric techniques. Optical densities of *P. ramorum* spore suspensions are measured to determine the effect of the chemical on sporangial germination.

Initial studies by Garbelotto *et al*. (2002) indicated that metalaxyl, copper sulphate and fosetyl-aluminium were effective against *P. ramorum* as they strongly inhibited mycelial growth in tests *in vitro*.

In the UK, a series of *in vitro* studies have determined that several chemicals may be effective against *P. ramorum*. Turner *et al*. (2004; 2006a; 2006b) tested the effectiveness of azoxystrobin, boscalid with pyraclostrobin, cyazofamid, etridiazole, fenamidone with mancozeb, famoxadone with cymoxanil, fenamidone with propamocarb hydrochloride, fosetyl-aluminium, fluazinam, mancozeb, mancozeb with dimethomorph, zoxamide or cymoxanil, metalaxyl-M, metalaxyl M mixed with fluazinam, mancozeb or chlorothalonil, propamocarb hydrochloride and tolyfluanid against European isolates. In amended agar tests, cyazofamid, etridiazole, fenamidone, mancozeb, metalaxyl-M and the metalaxyl-M mixtures were all found to be effective, similar results were obtained with the photometric assays for spore germination. Azoxystrobin and fluazinam, which were relativity ineffective against mycelial growth, were both far more effective against spore germination (Turner *et al*., 2004). Considerable differences in sensitivity were sometimes observed between isolates and evidence of resistance to metalaxyl-M was evident in one German isolate from *Rhododendron* (Turner *et al*., 2006a).

The effect of azoxystrobin, propamocarb hydrochloride, metalaxyl-M, mancozeb, cyazofamid and tolyfluanid on zoospore motility has been tested (Turner *et al*., 2006a). All except propamocarb hydrochloride showed activity against zoospore motility. The most effective ingredients were azoxystrobin, mancozeb and tolyfluanid. No evidence of metalaxyl-M resistance was observed in this experiment.

Heungens *et al*. (2005) tested a variety of chemicals using agar plate tests, these tests found that metalaxyl and dimethomorph showed complete inhibition of mycelial growth at 1 µg ml^{-1}. Cymoxanil, etridiazole and mancozeb caused growth inhibition at 10 to 100 µg ml^{-1}. Chlorothalonil, copper oxychloride, fenamidone, fluazinam, fosetyl-aluminium and propamocarb hydrochloride did not completely inhibit growth even at 100 µg ml^{-1}. Cyazofamid inhibited growth at a low concentration compared to the others but failed to completely inhibit growth at 100 µg ml^{-1}.

Wagner *et al*. (2007) found that dimethomorph, copper-octanoate and mancozeb with fenamidone were the most effective chemicals they tested showing complete inhibition of mycelial growth and zoospore germination. Azoxystrobin, cyazofamid and propamocarb hydrochloride were much less effective. Mancozeb and propineb showed less inhibition of mycelial growth but strongly reduced zoospore germination. Wagner *et al*. (2007) also

reported resistance for five European isolates to metalaxyl-M. These isolates all originated from nurseries. A study screening 85 European and 19 North American isolates for metalaxyl sensitivity (Wagner *et al*., 2006) found that 22.4 % of the European isolates were tolerant (i.e. less affected up to the threshold of 10 µg ml^{-1}). No North American isolates displayed tolerance to metalaxyl-M, but most of these isolates were isolated from natural habitats and probably had not been exposed to the fungicide before.

Yakabe and Macdonald (2007) tested chemicals in artificially infested soil in jars to determine their effectiveness as potential soil treatments. Chloropicrin, 1,3-dichloropropene, dichloropropene with chloropicrin, metam sodium, iodomethane, dazomet, dimethyldisulphite, peroxyacetic acid with hydrogen dioxide and zerotol were all tested. After two weeks or the 'label minimum re-entry period' (harvest interval), *P. ramorum* could not be detected in soils treated with chloropicrin, dichloropropene with chloropicrin, metam sodium, iodomethane or dazomet, whilst the remaining chemicals only reduced the number of viable propagules.

Effectiveness of chemicals as tested on detached plant material

Studies with plant material have obvious advantages. It is known that some compounds are more effective *in planta* and some chemicals do not work well in agar tests, for example due to binding. Also, with fosetyl-aluminium, phosphates and phosphonate treatments, which are all host stimulants, the active ingredient phosphorus acid is only released *in planta* (Garbelotto *et al*., 2002).

Chastagner *et al*. (2007) tested the effectiveness of 17 fungicides in protecting *Abies procera*, *Abies grandis* and *Rhododendron* species on detached seedling tops for the conifers and leaves for *Rhododendron*. The fungicides were applied prior to inoculation. They found mancozeb, mancozeb with zoxamide, dimethomorph, cyazofamid, maneb, polyram, fenamidone, chlorothalonil, fluopicolide and pyraclostrobin were the most effective chemicals in reducing disease on the conifer shoots. On *Rhododendron* they found that fewer of the 17 fungicides were effective, with maneb, mancozeb and zoxamide, and mefonoxam (which is known as Metalaxyl-M in the UK) being the most effective in controlling disease development on both wounded and non-wounded leaves.

Metalaxyl-M, mancozeb with dimethomorph, mancozeb with cymoxanil and mancozeb with fenamidone completely inhibited the development of disease symptoms when applied prior to inoculation in detached leaf assays on wounded rhododendron leaves (Turner *et al*., 2004).

Turner *et al*. (2006b) used *Rhododendron* and *Viburnum* detached leaf assays to test the effectiveness of cyazofamid, tolyfluanid, mancozeb with zoxamide, fenamidone with propamocarb hydrochloride, metalaxyl-M and metalaxyl-M mixed with fluazinam, mancozeb or chlorothalonil. Zoospores were used to inoculate the leaves 4 or 7 days before or after chemical treatments so protectant and curative activity were both assessed. As a

protectant at either timing, metalaxyl-M and mixtures containing metalaxyl-M prevented lesion development, as did fenamidone and propamocarb hydrochloride on both hosts. Azoxystrobin only prevented lesion development on *Viburnum*. There was no evidence of fungistatic activity, as *P. ramorum* was not recovered from leaves where the chemicals were 100% effective. However, incubation periods post-treatment were limited by the life span of the leaf. Shishkoff (2005) recovered *P. ramorum* after incubation for longer periods (see later). When applied as an eradicant, only products containing, metalaxyl-M halted lesion development. The pathogen could not be recovered (after ten days) from leaves following treatment with metalaxyl-M and mixtures containing metalaxyl-M. The pathogen was isolated from lesions following other treatments.

Effectiveness of chemicals as tested on whole plants: Tree hosts

Phosphonates are known to enhance the defence mechanism of trees against *Phytophthora* species, although the mode of action is not fully understood they are thought to combine a moderate direct antimicrobial property with the ability to trigger secondary metabolic pathways in the plant that are involved in antimicrobial response (Garbelotto, 2006). Phosphonates have been used successfully to treat trees infected with *Phytophthora cinnamoni* throughout the world (Guest *et al*., 1995). There have been various studies on the efficacy of phosphonates against *P. ramorum* in trees, some of these are described below.

Studies in the USA have evaluated the effectiveness of various chemicals in controlling the disease in trees. Garbelotto *et al*. (2002) tested several chemicals in 3m to 5m high potted saplings of *Q. agrifolia* inoculated with *P. ramorum*. All saplings were inoculated twice, approximately 11 weeks apart. Three days after the second inoculation, chemicals were injected into each sapling. They found that saplings treated with fosetyl-aluminium, metalaxyl and phosphoric acid had significantly smaller cankers than untreated saplings or those injected with copper sulphate pentahydrate.

Chastagner *et al*. (2005) tested the effectiveness of 20 fungicides in protecting Douglas-fir shoots from infection by *P. ramorum*. Of the fungicides applied before bud break, mefonoxam applied as a drench application was the only fungicide that prevented infection. Dimethomorph, pyraclostrobin and etridiazole all had no effect on the number of infected seedlings whilst phostrol (the active ingredient of phostrol is neutralised phosphorus acids) reduced infection by about 71 to 75%. Post-bud break applications of mancozeb, mancozeb with zoxamide, maneb and polyram provided 100% control. Applications of copper hydroxide, fenamidone, chlorothalonil, dimethomorph and cyazofamid reduced the number of infected seedlings by 70 to 100% but control was not consistent.

In a series of experiments between 2002 and 2004, phosphonate injections were found to be effective on 100% of potted oak (*Q. agrifolia, Q. parvula* var. *shrevei*) trees tested, while in the wild, 80 to 90% of the treated oaks and *L. densiflorus* responded positively to injections (Garbelotto, 2006). In these

experiments the trees were inoculated with the pathogen and both preventive and post inoculation treatments were tested. Preventative and early post-inoculation treatments were most effective and the efficacy of treatments declined as the amount of time between inoculation and treatments increased. Bark applications using an organosilicate adjuvant (Product name: Pentrabark) were found to be as effective as injections in potted trees and more effective than injections in the wild. However, Kanaskie *et al*. (2005) compared the efficacy of different treatment methods of one such phosphonate (Agrifos) (active ingredient mono and di- potassium phosphate) on *L. densiflorus*, either when injected into the sapwood or applied to trunks with organosilicate adjuvant. They found that lesion size was significantly smaller in trees injected with Agrifos than in the bark spray application with an adjuvant or untreated control trees. In these experiments the chemical was applied prior to inoculation.

Further field experiments have evaluated the effectiveness of Agrifos for control in *L. densiflorus* and *Q. parvula* var*. shrevei* (Schmidt *et al*., 2005). Native stands of mature, uninfected trees were treated with Agrifos and then inoculated with *P. ramorum*. Agrifos significantly reduced lesion size compared to untreated control trees. Using phosphonates may be useful in combating the disease on individual or small groups of valuable trees but it is unlikely to be practical on large numbers of infected trees.

Effectiveness of chemicals as tested on whole plants: Non-tree hosts

The use of Agrifos on ornamental plants has also been tested in the USA. Stringfellow and Reddy (2005a) found that treatments of Agrifos controlled ramorum blight on *Camellia japonica* with comparable efficacy to mefonoxam and dimethomorph. In these experiments plants were inoculated by keeping the plants near the inoculum source and Agrifos was then applied as spray alone, drench alone and spray/drench at monthly intervals.

Other US studies have tested the effectiveness of chemicals on non-tree hosts. Foliar applications of copper hydroxide prevented infection of *U. californica* for up to six weeks after treatment (Harnik and Garbelotto, 2005). Linderman and Davis (2005) tested various chemicals against infected *Rhododendron* and *S. vulgaris* leaves. Mefonoxam and the unregistered compound SA 110201 (Sipcam, Agro USA, Inc.) were found to be most effective, even 6 weeks after application. Orlikowski (2004a) found that furalaxyl applied 48 hours before or after inoculation of *Rhododendron* leaves and stems was the most effective treatment compared to fosetyl-aluminium, fenamidone with fosetyl-aluminium, propamocarb hydrochloride with fosetyl-aluminium, oxadixyl with mancozeb and cymoxanil with famoxate, although all the compounds tested significantly inhibited the development and spread of twig blight on rhododendron.

Tjosvold and Chambers (2005) evaluated cyazofamid, mefonoxam, dimethomorph, pyraclostrobin and fenamidone applied as foliar sprays to *Rhododendron*, *Camellia*, *Pieris* and *Viburnum* species on wounded and non-wounded leaves. The fungicides provided preventative activity as displayed

by a reduction in lesion sizes compared to control plants. Preventative activity lasted for up to two weeks for *Rhododendron* but up to four weeks for the other species tested. Post infection treatments of leaf lesions with foliar- and soil-applied fungicides were ineffective in reducing lesion development.

Turner *et al*. (2004) determined that azoxystrobin, metalaxyl-M and fenamidone with mancozeb completely inhibited symptom development on rhododendron when applied 7 or 4 days before inoculation. Cymoxanil with famoxadone and cymoxanil with mancozeb were most effective when applied seven days prior to inoculation whereas etridiazole and dimethomorph with mancozeb were more effective when applied four days before. Metalaxyl-M was the most effective treatment on *Viburnum* plants, completely inhibiting symptom development when applied four or seven days prior to inoculation. Mancozeb with dimethomorph and mancozeb with fenamidone were very effective when applied fours days before inoculation but their activity was much reduced when applied seven days before. When these treatments were applied four or seven days post inoculation, levels of control were generally lower than preventive treatments. However, metalaxyl-M (applied four days after inoculation) and etridiazole and mancozeb with fenamidone (seven days after inoculation) were most effective for *Rhododendron*. On *Viburnum*, azoxystrobin and metalaxyl applied four days after inoculation were most effective.

A later study by Turner *et al*. (2006b) tested the effectiveness of Citrox (a natural biocide from fruit acids), DP98 (nitrogen, potassium and phosphate) and fosetyl– aluminium on controlling the pathogen on rhododendron plants. The chemicals were applied 4 or 7 days before or after inoculation. None of the treatments at any of the application timings gave 100% control of *P. ramorum*. All treatments showed limited control of lesion development when applied as a protectant seven days before inoculation. Fosetyl-aluminium applied seven days after inoculation was the only treatment to show any eradicant activity.

Heungens *et al*. (2005) reported that on rhododendron plants, the fungicides that performed best on plants were metalaxyl, cyazofamid, and benthiavalicarb-isopropyl. Dimethomorph and fosetyl-aluminum had intermediate effects. Cymoxanil and mancozeb were the least effective of the products tested. Protective effects worked best when the lower surface of the leaf was covered with the fungicide, consistent with the observation that infection of non-wounded leaves inoculated with zoospores mostly occurs through the lower surface of the leaves. Curative fungicide treatments two days after zoospore inoculation were much less effective than protective treatments (1 day before zoospore inoculation). This indicated that curative applications of fungicides are difficult under optimal conditions for pathogen development. However, preventive use of fungicides can be very effective with selected fungicides, even under the conditions of high inoculum pressure.

Masking of symptoms by fungicides

It has been surmised that the use of fungicides can mask the development of symptoms. This would allow infected plants to evade visual detection during import inspections or during monitoring. Two studies indicate this is may not be a major factor but confirmatory evidence is still not available.

Shishkoff (2005) investigated whether fosetyl-aluminium, mefonoxam or propamocarb hydrochloride have a masking effect on infected *Rhododendron* shoots. The pathogen could be recovered from control (application of water), fosetyl-aluminium and propamocarb-treated lesions at high frequencies (64% or more attempted isolations successful) immediately after treatment but recovery declined afterwards. The pathogen was not recovered from mefonoxam-treated lesions until 3 to 5 weeks after treatment, and then only in low frequencies (below 13%). In all of the treatments, symptoms were not suppressed.

Turner *et al*. (2006b) found that following incubation of up to ten days, *P. ramorum* could not be recovered from leaves where the fungicide had been 100% effective, in both protectant and eradicant applications of metalaxyl-M, metalaxyl-M with fluazinam, metalaxyl-M with mancozeb, metalaxyl-M with chlorothalanil and propamocarb hydrochloride with fenamidone in detached leaf assays on *Rhododendron* and *Viburnum*. This indicated that the chemicals had killed the inoculum and was not merely fungistatic, though isolations were not made more than ten days after treatment.

Chemical treatment of water and soil

Chlorination of recycled water in nurseries is a common and effective practice that can control *Phytophthora* diseases. Surfactants (Yakabe and Macdonald, 2005), mefenoxam and Agrifos (Stringfellow and Reddy, 2005b) have also been shown to be effective for use on recycled irrigation water in the USA. Recent data from the UK has shown that hydrogen peroxide (as Jet 5) and sodium hypochlorite (10%) were effective (at label recommended rates) in decontaminating water inoculated with *P. ramorum* sporangia. Both products proved effective within five minutes exposure time (P. Jennings, 2007, *personal communication*).

Turner *et al*. (2006b) tested the efficacy of metalaxyl-M as a soil drench. Sterile compost was inoculated with *P. ramorum* sporangia and incubated for a week at 20ºC to allow growth. The pathogen could be isolated from all control and pre-treatment soil samples but was not isolated from post-treatment samples. This indicates that metalaxyl-M would be highly effective in soil but the authors state that it cannot be recommended alone due to risks of the development of resistance (which has subsequently been observed in Europe).

Basamid (350 lb/acre) was incorporated throughout the soil profile at three ornamental nurseries with infested sites in California (Yakabe and MacDonald, 2007). The beds were sealed with a polyethylene tarpaulin for 14 days. *Phytophthora ramorum* was not detected after treatment at any of the nurseries, two of the nurseries were not positive for *P. ramorum* in the

following year. The pathogen was detected at the third nursery the following year but the infested bed had no relation to the previously treated plot. Other nurseries in California that could not apply fumigants opted to treat their infested soil with hypochlorite, quaternary ammonia, or phosphites. In each case *P. ramorum* was detected after these treatments.

Chemical disinfectants

In the UK, chemical disinfectants are being used on nurseries for decontaminating plant standing areas, e.g. concrete, gravel beds or weed suppressant fabric, and other surfaces that have been in contact with infected plants. Their use is also recommended when undertaking eradication and containment activities in natural and semi-natural environments for the decontamination of footwear and tools that have come into contact with infected plants or soil.

Turner *et al*. (2004) tested Panacide-M, Hortisept, Virkon S and Jet 5 in a gravel/sand/soil mix and found that only Panacide-M at a rate of 1:60 was effective in eradicating *P. ramorum* after 48 hours exposure (contact time). Further experiments with Panacide-M, Dettol and Jeyes Fluid were done to determine the minimum period of exposure required to eradicate *P. ramorum* from a gravel/sand/soil substrate. Jeyes Fluid at a dilution of 30 ml l^{-1} was the most effective, having an effect after 10 minutes exposure. However, it was ineffective at a dilution of 7 ml l^{-1}. Panacide-M was fully effective at a dilution of 17 ml l^{-1} after 30 minutes exposure but ineffective at the lower concentration of 2 ml l^{-1}, even after 48 hours exposure. Dettol was effective at 25 ml l^{-1} after 4 hours, but was not recommended for use in outbreak situations, as the exposure time required would make its use impractical. Unpublished experiments by C. Lane (CSL) found that Panacide-M and Antec Farm Fluid S were effective in disinfecting a range of substrates including weed suppressant fabric, limestone chippings and wood after an exposure period of 10 minutes.

The activity of Panacide-M was tested for disinfection of an infested gravel pathway at an outbreak site in south-east England (Defra, 2007c). The path was tested for *P. ramorum* using baiting and quantitative-PCR methods prior to treatment with Panacide-M and at 24 hours post treatment and also two months later. All pre-treatment samples were positive for P*. ramorum* using both tests. PCR tests 24 hours post treatment showed that pathogen DNA was still detectable but no viable inoculum was detected using bait tests. Sampling two months later showed that inoculum levels had returned to similar levels observed prior to disinfection.

Since this work was completed the active ingredients of Jeyes Fluid have changed so its previous efficacy against *P. ramorum* can no longer be guaranteed. Panacide-M will be withdrawn on the 31 December 2007 and Antec Farm Fluid S was withdrawn from use in September 2006 as a result of the EU Biocides review.

The withdrawal of and changes to the products known to be effective against *P. ramorum* prompted further investigation of disinfectants for use on nurseries (CSL, unpublished data). This work suggested 70% industrial methylated spirits (IMS) was effective on a variety of surfaces provided that residual organic matter had been removed. Preliminary results have shown that both 70% IMS or Unifect G, after a 5 minute exposure time, effectively decontaminated weed suppressant fabric experimentally contaminated with *P. ramorum*. Jet 5, sodium hypochlorite and Menno Florades were also effective but required longer exposure times (30 min, 60 min and within 20 h respectively). All these disinfectants were inactivated in the presence of high levels of organic matter.

Another product 'Cleankill' (active ingredients: alkyl dimethyl benzyl ammonium chloride, didecyl dimethyl ammonium chloride and chlorhexidine digluconate) has been shown to be effective against *P. ramorum* (when grown on cellophane mats) after a 5 minute exposure time (J. Turner, *personal communication*). However, when tested for efficacy in the presence of organic matter, the product proved to be ineffective, with growth still recorded after 120 minutes exposure time.

Biological control

Biological control of a quarantine pathogen such as *P. ramorum* would not lead to its eradication. Biological control for plant pathogens is not widely used for non-quarantine disease control generally, with more conventional approaches (fungicides, host resistance, cultural control, rotation and good hygiene practice) being preferred by farmers and growers. Nonetheless a review of published work pertaining to biological control of *Phytophthora* species including *P. ramorum* is given below.

Biological control is yet to be proven successful for *P. ramorum* under field conditions. Various approaches are being investigated, from the more conventional use of mycoparasitic or antagonistic bacteria and fungi, to attempting to find viruses and extra-chromosomal elements that can affect *P. ramorum*. Work is also underway to determine if 'compost teas' (see description below), which may contain microbes antagonistic to *P. ramorum*, are effective. Natural plant products such as essential oils, plant extracts are also being trialled.

Bacillus brevis and *Paenibacillus polymyxa* inhibited the mycelial growth of several *Phytophthora* species, including *P. ramorum* in pure culture. However, these bacteria were unable to prevent disease symptoms occurring on detached leaves of *Rhododendron* and *S. vulgaris* inoculated with *P. ramorum* (Linderman and Davis, 2005).

Other studies with bacterial biological control agents have proven slightly more successful. A strain of *Pseudomonas fluorescens* is known to release a surfactant that can disrupt zoospore membranes in oomycete species. Applications of the bacteria prior to inoculation reduced *P. ramorum* infection in detached leaf tests on *U. californica* or *L. nobilis* but the results were highly

variable (Cohen *et al*., 2006). The treatment also conferred no apparent protection to seedlings of *U. californica*, *L. nobilis* and *L. densiflorus* placed in the under storey of *P. ramorum* infested *U. californica* trees during the rainy season. Elliot and Shamoun (2007) performed detached leaf assays using *Rhododendron* and *Camellia* leaves treated with various biological control agents 24 hours before wounding and inoculation with *P. ramorum*. They found that the bacteria *Streptomyces lydicus* strain WYEC 108 (Actinovate ®) and *Bacillus subtilus* both inhibited lesion development.

Widmer (2007) reported that several isolates of *Trichoderma* species were mycoparasitic to *P. ramorum in vitro*, attacking the sporangia and chlamydospores. A laboratory assay by Elliot and Shamoun (2007) also indicated this, and the authors suggest that *Trichoderma* could be effective in controlling the soil phase of the disease.

Widmer (2007) also reported that natural plant products could be effective. Caffeic acid added to V8 juice agar at concentrations of 1 g l^{-1} and 3 g l^{-1} inhibited zoospore germination *in vitro* by 98% or 100% respectively and sporangial germination was inhibited by 25% and 100%, also respectively. Rice bran extract containing derivatives of caffeic acid, was applied onto *Rhododendron* leaves prior to infection and was found to reduce leaf necrosis (Widmer, 2007).

Research is currently underway in Canada attempting to identify dsRNA viruses, plasmids and other cytoplasmic elements that can affect the pathogenicity of *P. ramorum* (Elliot *et al*., 2007).

The use of liquid teas made from composts (‘*compost teas*’) to try to protect susceptible plants against *P. ramorum* is reported to be gaining support amongst growers and home gardeners in the USA (Kliejunas, 2007). Compost teas are made by steeping compost in water, which can sometimes be amended with other natural ingredients. This is meant to encourage the growth of microbes that may inhibit pathogens. The teas are then directly applied to the foliage or soil. There is no published work on the use of compost teas to control *P. ramorum* specifically, although research is presently underway (Kliejunas, 2007).

Manter *et al*. (2006) reported that essential oils from cedars strongly inhibited zoospore germination and hyphal growth of *P. ramorum* in culture. Compounds from the heartwood of yellow cedar (*Chamaecyparis nootkatensis)* were also tested and displayed zoosporicidal activity and inhibition of hyphal growth. Heartwood shavings (stored dry) contained zoosporicidal active chemicals, leading the authors to suggest that spreading shaving or chips with appreciable concentrations of the zoosporicidal chemicals over areas of infection zones such as paths and areas used by hikers/cyclists may be useful as part of an integrated programme minimising the spread of *P. ramorum*.

Orlikowski (2004b) amended agar and soil leachate with grapefruit extract and found that this inhibited colony growth and sporulation of *P. ramorum*.

Spraying *Rhododendron* inoculated with *P. ramorum* was found to inhibit the spread of necrosis on stems and leaves. Pre- and post-inoculation spraying of *Rhododendron* with chitosan also suppressed the disease in this study.

Cultural control and environmental management

Cultivar resistance and production of clean plant material

A plant's degree of susceptibility or resistance to a particular pathogen is an inherited characteristic. This has allowed varieties of plants to be bred with resistance or reduced susceptibility to the pathogen. With other host-pathogen systems, breeding for resistance has, in parts, been successful. However, breeding for resistance in annual and biennial plants is generally easier than for woody perennials, such as shrubs or forest trees. At this stage, for *P. ramorum*, efforts are generally focused on determining if there is any resistance or reduced susceptibility to the pathogen within populations of susceptible hosts. If any is identified this may then prove to be useful starting material for any breeding programme. However, the wide host range of *P. ramorum* means that breeding for resistance is likely to be of limited use except for rare varieties.

Work in finding resistance to *P. ramorum* in trees has generally been done in the USA where varying levels of susceptibility to the pathogen has been found in *L. densiflorus, Q. agrifolia* and *U. californica*.

Hayden and Garbelotto (2005) observed variation among individuals and populations of *L. densiflorus,* suggesting that quantitative resistance to *P. ramorum* may exist in that species.

Dodd *et al*. (2005) found that the susceptibility of *Q. agrifolia* is variable and under the control of several gene loci. The authors suggested that this variation exists within populations, so less susceptible local genotypes could provide a gene pool for the regeneration of woodlands where mortality was high.

A wide range of susceptibility to foliar infection by *P. ramorum* has been observed for *U. californica* (Hüberli *et al*., 2002). Using detached leaf assays Meshriy *et al*. (2005) found that *U. californica* leaves from Oregon were generally less susceptible than leaves from California. Kliejunas (2007) suggested that thicker cuticles in the plants from Oregon could explain the difference, as they may reduce the potential for leaf infection.

In non-tree hosts, studies have observed differences in susceptibility of different cultivars or species of *Viburnum*, *Syringa vulgaris*, *Vaccinium* and *Rhododendron.* In detached leaf assays across 23 cultivars representing nine species of *Viburnum*, a range of susceptibility could be observed, from resistant to highly susceptible (Grünwald *et al*., 2005). Differences in cultivar susceptibility were also observed with *Syringa vulgaris* (Grünwald *et al*., 2006). Parke *et al*. (2002a; 2002b) observed a wide range of susceptibilities amongst species of *Vaccinium*, from the highly susceptible lingonberry

(*Vaccinium vitis-idaea*) to resistance in one cultivar of cranberry (the authors did not give the species name but cranberry is also in the genus *Vaccinium*).

For *Rhododendron*, De Dobelaere *et al.* (2005) screened wounded and non-wounded leaves and branches of 21 species and 42 hybrids. Differences in susceptibility were observed between species and hybrids. However, when wounded, most species and hybrids were susceptible to the pathogen. A larger variation in susceptibility was observed when no wounding was done, with little or no infection being observed in some hybrids. These results suggest that resistance could be related to the phenotype of the host tissue in preventing tissue penetration.

Micropropagation of at-risk, valuable specimen plants from historic gardens or national collections has been used successfully for preserving rhododendron, magnolia and camellia. (Ongoing Defra-funded Projects PHO316 and PHO418).

Manipulation of the growing environment

The following section describes effective practices and techniques to manipulate the growing environment to minimise the risk of *P. ramorum*. Practical advice for the nursery stock and garden centre industry can be found in Defra (2005d), this contains many techniques and best practices which can reduce the risk of *P. ramorum* being introduced onto a nursery and should it occur, measures which can reduce its impact. A sister publication for the guide is to be published shortly by Defra (2007e) and is aimed at semi-natural and natural environments. Various documents, e.g. best management practices (BMPs) are also available in the USA and Canada.

These documents describe best practices to reduce the risk of infection and spread of *P. ramorum*. For nurseries these include:

- The monitoring of susceptible hosts, particularly after damp, mild or rainy periods. Also monitoring site boundaries for any susceptible hosts and checking these periodically.
- Nurseries establishing quarantine areas for plants from external sources. This should be some distance away from susceptible hosts and requires nurseries keeping accurate records of all bought-in plant material.
- Maintaining good hygiene practices. This includes removing and destroying plant and leaf debris from beds housing susceptible material. Regular disinfection of tools, equipment, plant beds with appropriate products, keeping blocks of susceptible plants some distance apart, avoiding wounding plants (which are generally more susceptible) and propagating from disease-free material. Also, avoiding soil or container-soil contact with foliage as this can help reduce soil-borne infections. Raised benches, gravel or concrete floors could be utilised to minimise the risk.
- Blocks of susceptible plants can be alternated with known non-host plants.

The growing environment can also be manipulated to minimise risk of infection. *Phytophthora* species generally tend to thrive in relatively moist conditions. Reducing the available moisture would help reduce the chances of *Phytophthora* infection. Nursery beds can be raised in the centre to promote rapid drainage. Avoiding overhead irrigation would help minimise the chance of splash dispersal of the pathogen occurring. Splash dispersal of *Phytophthora* propagules from ground to foliage and from plant to plant can be an effective means of *Phytophthora* movement (Benson, 2003). Gravel surfaces have previously been proven to be very effective in preventing the splash dispersal of *Phytophthora* species (Kuske and Benson, 1983).

Studies are underway in Germany (Ufer *et al*., 2007) and the UK (Defra, 2006b) to determine the effectiveness of slow sand filtration systems to *P. ramorum* in irrigation water. These data show that slow sand filters are highly effective at removing phytophthora inoculum, including *P. ramorum*, from irrigation water. UV treatment may also be suitable (Benson, 2003).

Excessive applications of nitrogen to encourage lush rapid growth can result in foliage of *Rhododendron* or other hosts that is more susceptible to disease (Hoitink *et al*., 1986). Some potting mixes containing composted pine bark-based mixtures are known to naturally suppress *Phytophthora* species (Daughtery and Benson, 2005).

Some of these practices can also be applied for natural and semi-natural environments. There is evidence that the pathogen can be moved on footwear, mammals, and vehicles tyres. Therefore, site access could be restricted, particularly during high-risk periods (damp, mild and rainy periods). However, this is not always practical. Gravel pathways and grassing over and mulching may be useful in reducing the risk of transferring soil-borne inoculum.

Removal of infected plant material

The removal of susceptible under-storey foliar hosts from where susceptible trees are present could reduce the chances of tree infection occurring. Substantial sporulation has been observed in foliar infections on such hosts. In the UK, tree infection is typically associated with infected *Rhododendron* (Brasier and Jung, 2006). In California, abundance of *U. californica* has been shown to be associated with oak mortality (Kelly and Meentenmeyer, 2002; Swiecki, 2007). However, the removal of such hosts is often undesirable, impractical and expensive.

The fragmentation of woodlands by the removal of susceptible hosts may slow the spread and reduce the overall abundance of a pathogen such as *P. ramorum*. The data in Condenso and Meentemeyer (2007) supports this by indicating that *P. ramorum* disease severity is greater at locations surrounded by a high percentage of woodland habitat. Continuous swathes of host woodland provides more coverage area to intercept incoming pathogen propagules compared to smaller ones. Once invaded, large areas of woodland are likely to support higher disease levels as they are likely to

contain a greater number of susceptible hosts (Burdon *et al*., 1989). Plant removal also reduces canopy cover, at least temporarily, thereby increasing air movement and decreasing humidity, which may also reduce the spread of the pathogen throughout a given area. Conversely, Rizzo *et al*. (2005) speculated that the thinning of woodlands could increase airflow through stands and therefore actually facilitate dispersal of *P. ramorum* amongst trees by wind. It is also thought that the removal of forest habitat may have unexpected ecological effects and impacts on associated species (Condenso and Meentemeyer, 2007).

Evidence in the UK from at least two sites suggests that should an infection occur, rapid and thorough action involving removal of all infected plants (including, preferably, the residual stump and litter, and control of any re-growth, can be effective in reducing inoculum levels to below the current threshold for detection (Turner *et al*., 2007). In these UK studies, removal of infected plants at one SE England site has resulted in no new plant infections since 2003. At all outbreak sites, inoculum is still detectable in soil and water, but where action has been thorough, levels of residual inoculum appear to be at epidemiologically insignificant levels.

US evidence for the benefits of taking eradication activity involving the removal of infected hosts can be assessed by comparing the development of the epidemic in Curry County, Oregon (where eradication activities have included the removal of infected trees and plants) and Humboldt County in California, where eradication was not carried out. Infection was first observed in these areas in 2001. However, as of 2006, only 128 acres of Curry County in Oregon have been recorded with infection, whereas the disease has been recorded in 3,853 acres in Humboldt (Kanaskie *et al*., 2007). It is interesting to note that as of 2004, infection was only observed in 123 acres of Humboldt County, rising to 2,268 in 2005 (Hansen, 2007). This may be evidence that once the population of *P. ramorum* reaches a critical threshold, a sudden and large increase in infection could be observed. However, this is by no means certain; differences could be due to forest vegetation, weather, or other factors. This is an important consideration when considering the future impact of the pathogen.

Pruning of infected areas of tree and large plants can sometimes be undertaken in order to excise the infection, for instance where a particular branch is infected (Defra, 2007d). This would be particularly useful for historical or valuable trees or in small scale plantings, perhaps combined with the use of fungicides during the pruning actions to protect wounded tissues.

At present, total removal of phloem and outer bark from tree stems is a recommended procedure for preventing the spread of quarantine pathogens such as *P. ramorum* on transported wood products. Recent findings by Brown and Brasier (2007) shows that *Phytophthora* species, such as *P. ramorum,* can remain active and viable up to 25 mm into the xylem. The authors suggest a more stringent treatment is required to prevent risk of spread, the minimum being the removal of 3cm of outer sapwood but this may be

impractical, hence the destruction of infected tree stems may be the preferred option.

Heat treatment

Heat treatments are being investigated to determine the efficacy of eradicating *P. ramorum* from infested host material. Harnik *et al*. (2004) found that *P. ramorum* can be highly heat tolerant. They were able to re-isolate from artificially inoculated California bay laurel (*U. californica*) leaves held at 55°C for up to 1 week. The pathogen was not recovered after 2 weeks at that temperature. However, such prolonged heat treatment is impractical for California bay laurel leaves intended for commercial sale, so a gradual and progressive heating process was developed, combined with the application of a moderate vacuum. This treatment could be completed in 22 hours and eliminated the recovery of *P. ramorum* with no adverse effect on the quality of the leaves.

Linderman and Davis (2006) found that steam (wet heat) is more effective than dry heat treatments. They found that aerated steam pasteurisation at 50°C or higher for 30 minutes eradicated *P. ramorum* as well as other pathogens from infested soil-free potting media and contaminated containers, without destroying the containers.

Preliminary data from Tubajika *et al*. (2007) found that a treatment at 56°C for 30 minutes might not be adequate to kill *P. ramorum* in wood. However, the results were inconclusive, particularly because the detection of *P. ramorum* in the controls was low.

UK studies have determined the effectiveness of heat treatments for *P. ramorum* on rhododendron, viburnum and camellia. A range of dry and wet heat treatments were tested in one project (Turner *et al*., 2006c). The experimental work on mycelia and sporangia indicated that a 30-minute dry heat treatment at 60°C was required to achieve complete kill for *P. ramorum*. However, rhododendron, viburnum and camellia plants were completely killed after a 20 minute dry heat treatment at 55°C. Further experiments were carried out on detached leaves using a longer treatment period (130 minutes at 45°C) and whilst this did have an adverse effect on *P. ramorum* infections. However when the experiment was repeated using whole plants the treatment was ineffective in controlling symptom development. (P. Jennings, Unpublished). Further work would be needed to optimise this process before it could be used to treat the pathogen in nursery situations.

Composting

Composting may be an effective treatment for *P. ramorum*-infected plant material (Garbelotto, 2003). However, where chlamydospores are present it may not be possible to determine their viability post-composting via traditional baiting methods as they may be dormant rather than dead. Experiments by Swain *et al*. (2006) indicate that appropriate composting can effectively eliminate *P. ramorum* from green-waste. In laboratory tests the pathogen

could not be isolated from infested wood chips and cankered stems of *U. californica* and *Q. agrifolia* after a two-week exposure at 55°C. In field composting trials both with windrow and forced-air methods, the same type of material was considered *P. ramorum* free after two weeks. This was confirmed by isolation and by PCR assay. The absence of *P. ramorum* DNA led the authors to conclude that the pathogen was absent and not merely suppressed or dormant. More recently, Chimento and Garbelotto (2007) developed a new RT-PCR method which detects mRNA as a viability marker. This method has shown that after 9 days, RNA of freeze-dried killed *P. ramorum* in leaves of *U. californica* was undetectable while DNA gave a positive signal. This new method would be usefully-deployed to validate the earlier work of Swain *et al*., 2006, in order to determine whether mRNA remained viable after composting infected plant material when DNA-testing is negative. If this is the case then composting may not be suitable proposition for composting plant material infected with *P. ramorum*. Whilst *P. ramorum* is subject to statutory controls, composting is currently not used as a disposal method in the UK.

PHYTOSANITARY RISK

Nurseries

Since official surveys began (2002 for the EU and 2001 for the UK) *P. ramorum* has been found affecting a wide-range of host species in 14 plant genera at nurseries in 15 EU Member States (Slawson *et al*, 2007). Numerous nurseries in a wide-range of locations have also become affected by *P. ramorum* in the USA, and to a much lesser extent in Canada, following a large increase in findings related to shipments from a large wholesale nursery in California in 2004 (Suslow, 2005). Surveillance of the pathogen in the EU has shown that the pathogen can survive in nurseries, but also that the EU phytosanitary measures are reducing the numbers of new outbreaks on commercial premises (Slawson *et al*., 2007) and reducing the amount of infected material moving in trade within the EU. The wide host range, coupled with the survivability of the pathogen means that it is likely to continue to persist and establish in European nursery environments, throughout most of the EU if it is not controlled.

Phytophthora ramorum adversely affects the production of ornamental plants and trees by causing visual symptoms, thus affecting quality and in some instances may result in plant mortality. In severe outbreaks, *P. ramorum* can cause economic loss through the destruction of nursery stock due to severe infection; in addition to the financial value of the plants that have been destroyed, there are associated increases in costs of production. Whilst the pathogen is regulated, its presence at a place of production affects domestic and international trade. Many countries list *P. ramorum* on either their regulated pest lists or in their legislation (listed in Appendix 5). However, this effect is unlikely to be severe in the UK. as the value of exports for *Rhododendron* and *Azalea* was £38,000 (Defra, 2006a). No information on international trade of hardy ornamental stock is available for other EU

Member States but the Netherlands in particular has a large import and export market for ornamental plants.

Chemical control options are available to manage *Phytophthora* diseases in a nursery setting. Such chemicals are already used to control other species of *Phytophthora*, along with other foliar fungal pathogens. However, there is potential for *P. ramorum* to develop resistance to some chemicals, particularly those containing metalaxyl so their use must always be considered carefully and used in a sustainable fashion with other products. In a nursery setting, cultural and hygiene measures are likely to reduce the potential risks of spreading the pathogen. However, the difference between this pathogen and other nursery pathogens is the higher potential risk it poses to trees and ornamental hosts in natural and semi-natural environments, as well as to those hosts established in gardens involved in tourism, and also heathland plants.

Established plants

In Europe, the pathogen has a limited distribution outside of nursery environments but its increasing presence in natural and semi-natural environments means that a definite pathway into these environments exists and that the pathogen can establish in such environments. However, in most EU Member States where it is present in natural or semi-natural environments, it is only found on ornamental hosts. It is only in the UK and the Netherlands where it has been found causing bleeding cankers on mature trees (some of which have died) but there are relatively few trees compared to the situation in California, where over a million trees have been killed. Eradication is being attempted in some of the affected locations in the UK, principally by the removal of infected *R. ponticum* in woodlands; evidence has shown a reduction in new infections following removal even though the pathogen can still be detected in the environment (Defra, 2007d). The full potential of *P. ramorum* is yet to be realised.

Based upon our present knowledge of the pathogen, one, or a combination of the reasons below could explain the differences in tree mortality between Europe and North America. These reasons could include:

- Climate differences between Europe and North America. However, climatic mapping (R. Baker, *personal communication*) has shown that significant similarities exist between the Californian/Oregon climate where tree death has been observed and parts of Europe, such as the south-west of the UK, or Portugal (where the pathogen has not been found). The topography of California is such that the coastal valleys and hills are more extensive and this may be one of the factors favouring the pathogen there.

- Differences in host species and host associations/communities. The species of tree bleeding canker hosts and under-storey hosts differs between North America and Europe. For example, evergreen *L. densiflorus* (tanoak) was one of the tree species most severely affected

by *P. ramorum* in the USA, and is not grown widely in Europe. Also, *U. californica* (Californian bay laurel), another epidemiologically significant evergreen foliar host that produces large amounts of *P. ramorum* inoculum, does not grow in European woodlands or forests (CABI, 2007). In the UK, the most significant foliar host producing inoculum that might threaten susceptible trees is rhododendron, especially *R. ponticum.* The risk to susceptible trees will almost certainly be related to their proximity to infected rhododendron, the density of infected rhododendron, and climate/micro-climate; other evergreen foliar hosts might also be significant, but most likely to a much lesser degree in terms of initiating and maintaining epidemics on trees.

- Levels of inoculum may be lower in European woodlands and forests than in North American locations and thresholds for infection may potentially differ between European and North American tree species. It is likely that there is a threshold of inoculum needed before trees become widely infected. Inoculum levels in Europe may not have reached the critical levels required for widespread tree infection to occur. Inoculum levels may be lower because the pathogen has been present in Europe for a shorter amount of time, or eradication efforts have been successful in reducing inoculum, or several of the North American host plant species can support higher levels of *P. ramorum* sporulation than European hosts such as *R. ponticum*, thereby producing higher levels of inoculum in the environment. However, the UK climate is likely to support pathogen activity on foliar hosts (i.e. sporulation) throughout the year, whereas in California it is more or less restricted to the cooler/wetter parts of the year (mainly winter/spring).

- Differences in the pathogen population. The majority of isolates in North America are genetically different to the European population (Ivors *et al*., 2006). Differences in pathogenicity have been observed. In pathogenicity tests on the American red oak (*Q. rubra*), EU isolates were on average significantly more aggressive than US isolates (Brasier *et al*., 2006). EU isolates were found to be more aggressive than US isolates in pathogenicity tests on rhododendron stems (Werres and Kaminski, 2005). Differences in growth rate and colony type have also been observed (Brasier *et al*., 2006; Ivors *et al*., 2006; Werres and Kaminski, 2005).

Risks to the established plants in relation to nursery outbreaks

Currently, when *P. ramorum* is found in nursery environments in the UK/EU, statutory action is required to eradicate the pathogen. Other measures are also in place to reduce spread of the pathogen during trade in ornamental nursery plants. In the UK, the number of positive inspections and the number of newly infected nurseries is declining (Slawson *et al*., 2007). Modelling work has suggested that if the UK nursery trade in hardy ornamental nursery stock fits a scale-free network dominated by super-connected nodes, then such a network has the advantage that focusing controls on these nodes (e.g.

wholesaler nurseries) would be cost-effective in preventing spread of *P. ramorum.* However, the structure of the UK hardy ornamental nursery network is currently unknown. (Jeger *et al*., 2007). Modelling work also suggests that the correlation coefficient between links in and out of nurseries has a fundamental influence on the epidemic threshold. Scale-free networks only have a lower epidemic threshold than other kinds of complex networks if the risk of spreading *P. ramorum* from a given nursery to others is correlated to the risk of acquiring the pathogen for that given nursery from other ones (Pautasso & Jeger 2008). However, this key information is currently unknown for UK nurseries.

It is probable that if measures were to be relaxed, *P. ramorum would* become more widespread and have a higher incidence and severity in the nursery trade, thereby increasing risks of spread to established plants into the natural or semi-natural environment.

A recent study in the USA determined that there was greater genetic diversity in isolates from nurseries than in natural environments (Ivors *et al*. 2006). Therefore, should the disease be managed poorly in the nursery trade, it is likely that this will increase the risk of further introductions of the pathogen to natural and semi-natural environments. An increased presence of the pathogen in natural and semi-natural environments will not only increase the risk of tree infection, but could increase the total genetic diversity of the pathogen in such environments. It could also increase the chance of recombination by bringing together isolates of the different mating types. If the breeding system is viable, and this is still uncertain, this would lead to the formation of thick-walled, potentially long-lived oospores, which would result in the pathogen being more resilient to unfavourable environmental conditions, but also increase the total genetic diversity and adaptive behaviour/fitness of the pathogen population . This would allow greater potential for the pathogen to develop increased aggressiveness towards host plants, increase its host range and may increase its ability to develop resistance to chemicals, all of which would increase the risk posed by *P. ramorum*. Environments at risk include nurseries, forests, parks and gardens, and also heathland, where the pathogen has not been observed to date, but where experimental testing has found that some species found in this habitat are highly susceptible (Defra, 2005b).

Presently, only three A2 isolates of the European lineage have been found in Europe to date and these were all found on ornamental hosts in Belgium. Both mating types have also been observed in the US but only in nurseries with the EU1 (A1) and the NA2 (A2) being found several times in the same nurseries. Therefore to date, there has only been limited opportunity for both mating types to be present, reducing the potential for sexual hybridisation to occur.

There may also be a risk of *P. ramorum* hybridising with other *Phytophthora* pathogens. This has occurred with other *Phytophthora* species, and can give rise to completely new organisms that exhibit new host ranges. An example of this is the new hybrid species, *Phytophthora alni*, which is associated with the

death of alder trees throughout the UK and Europe (Brasier *et al*., 1999; Brasier *et al*., 2004c). *Phytophthora ramorum* has been found in close vicinity to other *Phytophthora* species including *P. kernoviae*, *Phytophthora ilicis* and other well known established *Phytophthora* pathogens such as *P. cambivora* and *P. citricola* (Brasier, 2003). Therefore, geographically, *P. ramorum* has an opportunity to hybridise with other *Phytophthora* species but it remains to be seen if the organism is biologically capable of doing so. The potential for *P. ramorum* to hybridise with other *Phytophthora* species is being investigated in a Defra-funded project (Defra, 2006c).

Although phytosanitary measures are currently in place to reduce the risk of entry into and spread of the pathogen within the EU on plant material, this could occur through infested bark, logs, cut wood and possibly seeds of a range of hosts. As this pathogen is an introduced exotic pathogen of unknown origin (Asia is a possible origin), it is also possible for new isolates/populations to be introduced from other unidentified sources.

PHYTOSANITARY MEASURES

Existing phytosanitary measures in place in Europe and North American countries are reviewed below. These have been reviewed in further detail in Steeghs (2007) and are summarised below.

Current EC Phytosanitary measures

In the European Union (EU), phytosanitary measures are being taken against *Phytophthora ramorum* to protect parks, gardens, nurseries and woodlands. The measures attempt to prevent the entry into and spread of the organism within these environments and are based upon controls on known host plants at the place of production and their subsequent movement. There is also a requirement for surveillance for the presence or absence of *P. ramorum* in EU Member States.

In the case of a finding at a place of production (nurseries) the following is required as a minimum:

- Destruction of infected plants and all susceptible plants within a 2 m radius of the infected plants (from May 2007 this will include the destruction of associated growing media and plant debris).
- A quarantine period of three months of active growth for all susceptible plants within 10 m of the infected plants and any remaining plants from the affected batch.
- For plants under quarantine, treatments that might suppress symptom development are prohibited during the quarantine period.
- For plants under quarantine, at least two official inspections must be carried-out during the quarantine period.
- All other susceptible plants at the place of production should be subject to intensive official re-inspection during this period (from May 2007, appropriate phytosanitary measures will have to be taken on the growing surface within a 2 m radius of infected plants).

Additional measures that have been taken by individual Member States include:

- No treatment that could suppress symptoms should be applied during the quarantine period for all susceptible plants at the place of production.
- Where the infected plant is soil-grown, no host plant may be grown in the same area or the area immediately surrounding an infected plant for 3 years.
- A survey of plants within a 500 m radius around an infested place of production
- After a finding, regular checks of all other susceptible plants at the place of production, including testing of plants and soil.
- Hygiene measures for container-grown plants, disinfection/destruction of cloth, pots and any other associated material.

Within the EU, plant health checks are focused on the place of production. There are no border checks for plants and plant products moving between EU member states. However, *Camellia, Viburnum* and *Rhododendron* (excluding *Rhododendron simsii*) are included in the plant passporting regime, and material from these species requires a plant passport to facilitate its movement at all stages down to the final retailer. The passport is needed both for movements within and between Member States.

An evaluation of the efficacy of the EC emergency phytosanitary measures (introduced in 2002) on the incidence of new outbreaks on commercial premises was made by Slawson *et al*., 2007. It was found that the number of new outbreaks on nurseries and retail premises declined from 255 in 2004, to 203 in 2005 and 108 in 2006. Analysis of the number of new outbreaks in England and Wales showed a variable number between 2002 and 2006 with no particular trend; however the peak number of new findings was made in 2003 (161) and the lowest in 2006 (34). The pathogen continued to be found in the EU on commercially-traded plants. The tentative conclusion was that rigorously applied official measures can reduce the incidence of *P. ramorum* moving in the nursery trade.
With regard to findings of the pathogen in natural and semi-natural environments, the only official requirement is that appropriate measures need to be taken to at least contain the harmful organism. Measures used in the EU include prohibition on the movement of infected plants and parts of plants, destruction by removing and burning, deep burial (this may have to be away from the affected site in approved landfill in the UK) or composting (not allowed in the UK) of the plant material, prevention of regrowth, and restricting access to the outbreak area.

If more than just a few plants are affected then outbreaks in natural and semi-natural environments are generally more difficult to eradicate than outbreaks in nurseries and garden centres. The resources required for removing or cutting back plants, removing and treating plant debris, control of subsequent regrowth, hygiene measures and restrictions in access are often substantial and are required over long periods. In the Netherlands and the UK, it is accepted that in those cases where eradication measures cannot be

achieved, containment measures are taken, in line with EC emergency measures. These aim to prevent spread of the pathogen from within a delimited area so that other susceptible host plants do not become infected. Such containment practices can include creating a buffer zone around the outbreak by removing host plants within a certain distance of the edge of the outbreak, prohibition of the removal of plant material, reducing the inoculum pressure by creating an environment which is unfavourable to the pathogen, and, restrictions in access to the affected area to prevent outward spread (Steeghs, 2007). The removal of infected *R. ponticum* (rhododendron) from woodland can result in a reduction of inoculum in the environment and protection of uninfected plants/trees. This has been shown at two woodland sites in southeast England (Defra, 2007d). This approach could be considered in any future phytosanitary measures for woodland/forest environments.

US and Canadian Phytosanitary measures

The pathogen has been detected in nurseries in at least 20 states in the USA and at a few nurseries in British Columbia, Canada. It has been detected in forests in California and Oregon. Phytosanitary measures for Canada (Anon., 2006c) are in line with the USDA 'confirmed nursery protocol' (Anon., 2007b).

The main differences between the North American and the EC legislation are that in North America:

- The tracing is more extensive (all host plants shipped within North America) and over a longer period (12 months).
- Extensive surveillance in the perimeter of the infested nursery.
- The destruction of plants is not limited to the infected plants and the remaining host plants in a radius of 2m. All hosts and associated hosts neighbouring the infected hosts are destroyed until a 2m break occurs in the host material.
- More emphasis is given to testing of planting material, soil and water.
- Nurseries are only released from regulation if no additional *P. ramorum* is found in the nursery stock, water, soil and growing media.

In natural and semi-natural environments in the USA, the "*Phytophthora ramorum* APHIS Response Protocol For Forest and Wildland Environments" (Anon., 2006d) is applied. The pathogen has not been found in such environments in Canada. Measures in the US Protocol include:

- Measures must be initiated to prevent movement of infected plant material.
- If the pathogen has been recently introduced, and its distribution remains limited, the resulting action may be similar to that undertaken following a finding in a nursery setting. In nurseries all hosts and associated hosts contiguous with the infected hosts are destroyed until a 2m break occurs in the host material. A 10m radius surrounding that is placed on hold for at least 90 days.
- Where the outbreak is larger, with secondary spread having occurred from the original source, a more rigorous response is appropriate. For an established outbreak, a quarter-mile buffer area around the known

infected material is established and plant material within it is prohibited from movement pending a delimiting survey. Equipment on site and within the quarter-mile buffer has to be properly cleaned and/or decontaminated prior to being moved.

- Containment of the pathogen is taken when eradication is not feasible.
- Eradication measures for established outbreaks require removal of infected and uninfected host plants within 100 ft (30.48m) of an infected plant.

APHIS also have a protocol for residential landscapes (APHIS, 2004).

Presently, eradication efforts at forest sites are no longer considered feasible in parts of California. Eradication efforts in forestland in Curry County, Oregon have been undertaken since its discovery there in 2001. Action taken includes cutting and burning all infected and nearby host plants. On private land, stumps and sprouts of host vegetation are treated with herbicide to kill sprouts and prevent future sprouting. The distribution of the pathogen in Oregon appears to be limited, suggesting that the eradication effort has significantly slowed the progress of the pathogen (Hansen, 2007), but efforts to eradicate the pathogen from Oregon forests likely are continue for several years (Kanaskie *et al*., 2007).

CONCLUSIONS

Phytophthora ramorum is a plant pathogen that is considered to be a relatively recent exotic introduction to the UK, the EU and to North America, speculated but not proven to originate in Asia. It is relatively widely distributed, but at low incidence, in the UK and EU nursery trade. It has also been recorded on nurseries in the USA and British Columbia, Canada.

It is present in the outdoor environment on established plants in a number of EU Member States but is of particular concern in the UK and the Netherlands where it is more widespread in the natural or semi-natural environment on foliar hosts such as rhododendron and where a small, but increasing, number of trees have developed bleeding cankers especially beech (*Fagus sylvatica*) and several species of oak (*Quercus* spp.); some trees have died. By contrast, the pathogen has caused massive numbers of tree deaths in California and a lesser number in Oregon, USA.

Phytophthora ramorum continues to pose a threat to the managed and unmanaged environment (woodlands; gardens; heathland), the timber and ornamental plant trade and the tourism industry (e.g. associated with historic gardens) in the UK, EU, North America and to other countries where it is yet to be reported or introduced.

Phytophthora ramorum is subject to regulation and phytosanitary measures in the UK, EU and North America (including import controls) and is subject to import controls in a number of other countries.

It may not be possible to eradicate *P. ramorum* completely from the semi-natural or natural environments outside of nurseries but it is possible to reduce the level of inoculum to epidemiologically insignificant levels by removal of foliar hosts, especially invasive *Rhododendron ponticum*. Foliar hosts are central to the epidemiology of *P. ramorum* since they are responsible for the production of inoculum, which then poses a potential threat to susceptible trees. Removal of these foliar hosts will help prevent further spread beyond the currently affected areas of the UK and will help to protect susceptible trees and other host plants. However, it requires a long-term commitment.

An environmental epidemic on the scale of the USA is yet to be witnessed in the UK or in other EU Member States. Tree mortality is probably unlikely to occur to the same extent, mainly because plant communities are different. California woodlands have a highly diverse plant community, which includes several key evergreen foliar hosts that produce large amounts of inoculum that infect and kill highly susceptible oak species. In the UK and Europe, the distribution of foliar 'sporulating' hosts (especially *R. ponticum*) in relation to susceptible trees is less correlated, though significant numbers of susceptible trees (especially beech) are found in close association with *R. ponticum* in the UK, in areas that are climatically suitable; native 'white' oaks (e.g. *Q. robur* and *Q. petraea*) are less susceptible than American red oak species such as *Q. agrifolia*. There is a difference in scale of the coastal valleys and hills in California compared to the UK. However, environmental conditions may be more favourable in the UK than California as the climate is cooler during the summer, potentially facilitating inoculum production throughout the year. European isolates of *P. ramorum* have been shown to be generally more aggressive than US isolates, which may increase the potential risk. There also remains the potential for an increase in genetic diversity and adaptive fitness in the European population by the introduction of non-European isolates of the opposite mating type to the main population, but it is still not certain whether the breeding system of *P. ramorum* is fully functional. However, genetic recombination can occur through somatic hybridisation and so this cannot be ruled-out.

The current indications are that *P. ramorum* is likely to continue to be locally damaging in the UK and possibly in other EU Member States including the Netherlands, especially in managed ornamental gardens with established susceptible plants, or woodlands infested with rhododendron, especially *R. ponticum*, and coastal valleys in the south and west of the UK. The finding of a single beech tree and infected *R. ponticum* at a managed garden in West Yorkshire in late October 2007 may indicate an increased potential area of distribution related to the exceptionally wet summer in this and other locations.

There is evidence that the EU phytosanitary measures are reducing the number of new outbreaks on nurseries; in the UK.

There is also evidence that removal of infected *R. ponticum* from woodlands can protect trees from infection by reducing the level of inoculum, potentially below epidemiological significant levels or thresholds.

Although the costs and benefits of the measures are yet to be fully determined, current evidence indicates that it would seem appropriate to review and consider continuing with the current measures, i.e.:

(i) Continued controls on susceptible plants imported from the USA to prevent the introduction and spread of isolates of the North American populations;
(ii) Continued Plant Passporting controls on the key hosts moving in the EU nursery trade to prevent further introduction and spread, both within the trade and into the environment;
(iii) Continued action against infected plants on nurseries;
(iv) Continued action (containment and eradication) of outbreaks in the environment, e.g. continued clearance of rhododendron and other natural hosts from affected woodlands/gardens to reduce inoculum loads and the risks to trees and other important plant genera. Consideration would need to be given to funding an intensive programme for total removal of *R. ponticum* within woodlands including follow-up action to prevent sprouting of stumps, or removal of stumps altogether. Control of newly-emerged seedlings of *R. ponticum* will also need to be undertaken
(v) That timber from known infected trees continues to be destroyed rather than allowing it to be used so as to prevent the (low) risk of distribution of *P. ramorum* with infected wood

Further consideration of phytosanitary measures will be undertaken in the new Pest Risk Analysis for the EU, which will be derived from the information presented in this new Datasheet, the findings of the EU research project RAPRA, and by an EC review of the current EC emergency measures in 2008.

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Appendix 1. A list of natural hosts with symptom and location

Family	Latin name	Common name	Damage type*			Location(s)†	References
			F	D	C		
Aceraceae	*Acer circinatum*	Vine maple	✔			USA (outdoor)	COMTF (undated)
	Acer davidii	Striped bark maple	✔			Canada (nursery)	COMTF (undated)
	Acer macrophyllum[1]	Big leaf maple	✔			USA (outdoor)	Garbelotto *et al*. (2003)
	Acer laevigatum	Evergreen maple	✔			UK (outdoor)	Forest Research records
	Acer pseudoplatanus[1]	Sycamore			✔	UK (outdoor)	Forest Research records
Anacardaceae	*Toxicodendron diversilobum*	Pacific poison oak	✔		✔	USA (outdoor)	Rizzo (2003)
Apiaceae	*Osmorhiza berteroi*	Sweet cicely	✔			USA (outdoor)	COMTF (undated)
Apocynaceae	*Nerium oleander*	Oleander	✔			USA (nursery)	COMTF (undated)
Aquifoliaceae	*Ilex purpurea*	Oriental holly	✔			Canada (nursery)	APHIS records
Berberidaceae	*Vancouveria planipetala*	Redwood ivy	✔			USA (outdoor)	COMTF (undated)
Betulaceae	*Corylus cornuta*	California hazelnut		✔		USA (outdoor)	Murphy & Rizzo (2002)
Calycanthaceae	*Calycanthus occidentalis*	Spicebush, western sweetshrub	✔			USA (outdoor)	COMTF (undated)
Caprifoliaceae	*Lonicera hispidula*[1]	Californian honeysuckle	✔			UK (nursery)[2], USA (outdoor)	Garbelotto *et al*. (2003), CSL records
	Lonicera periclymenum	Honeysuckle	✔			Canada (nursery)	CFIA records
	Viburnum spp.[1]	Viburnum	✔	✔		UK (nursery and outdoor), Belgium (nursery), the Czech Republic (nursery), France (nursery), Germany (nursery), Ireland (nursery), the Netherlands (nursery), Norway (outdoor), Slovenia (nursery and outdoor), Spain (nursery), Switzerland (nursery and outdoor), Canada (nursery), USA, (nursery).	Lane *et al*. (2003), Cahalane (2004), De Merlier *et al*. (2003), Běhalová (2006), Werres *et al*. (2001), Pintos Varela *et al*. (2004), Žerjav *et al*. (2004), Heiniger *et al*. (2004), RAPRA (undated), COMTF (undated), Anon. (2006a) Parke *et al*. (2004).

*F = Ramorum leaf blight (including petiole), D = Ramorum dieback, C = Ramorum canker
†Also includes situation: nursery and/or outdoor
[1] Koch's postulates have been successfully completed for this host
[2] These records refer to interceptions on nursery stock. The country given is where the infected plant was found but the plants were originally grown in another country that is not named here.
[3] The *Schima* sp. record is not yet identified to species level, possibly *Schima yunnanensis*
[4] Symptoms not known

Family	Latin name	Common name	Damage type*			Location(s)†	References
			F	D	C		
Celastraceae	*Euonymus kiautschovicus*	Spreading euonymus, creeping strawberry bush	✔	✔		Canada (nursery)	CFIA records
Cornaceae	*Griselinia littoralis*[1]	New Zealand privet	✔	✔		UK (outdoor)	Giltrap *et al.* (2006)
	Cornus kousa x *Cornus capitata*	Cornus Norman Haddon		✔		UK (outdoor)	Forest Research records
Dryopteridiaceae	*Dryopteris arguta*	Californian wood fern, coastal woodfern	✔			USA (outdoor)	COMTF (undated)
Ericaceae	*Arbutus menziesii*[1]	Madrone	✔	✔		USA (outdoor)	Garbelotto *et al.* (2003)
	Arbutus unedo	Strawberry tree	✔	✔		Guernsey (nursery), Spain (nursery)	CSL records, COMTF (undated)
	Arctostaphylos columbiana	Hairy manzanita	✔	✔		USA (outdoor)	COMTF (undated)
	Arctostaphylos manzanita[1]	Manzanita	✔	✔		USA (outdoor)	Garbelotto *et al.* (2003)
	Arctostaphylos uva-ursi	Kinnikinnik, bearberry	✔			USA (nursery)	COMTF (undated)
	Calluna vulgaris[1]	Heather		✔		Poland (nursery)	Orlikowski & Szkuta (2004)
	Gaultheria shallon	Salal, Oregon wintergreen	✔			Canada (nursery)	CFIA records
	Kalmia sp.	Species not presently known				Canada (nursery)	CFIA records
	Kalmia angustifolia	Sheep laurel	✔	✔		UK (nursery)[2]	CSL records
	Kalmia latifolia[1]	Mountain laurel	✔	✔		UK (outdoor and nursery), Slovenia (nursery)	CSL records, RAPRA (undated)
	Leucothoe axillaris	Fetter-bush, dog hobble	✔			Canada (nursery)	COMTF (undated)
	Leucothoe fontanesiana[1]	Drooping leucothoe	✔			UK (nursery)	CSL records
	Pieris sp.	Species not presently known	✔			Canada (nursery)	CFIA records
	Pieris floribunda x *japonica*[1]	Mountain andromeda	✔	✔		USA (nursery)	Parke *et al.* (2004)
	Pieris formosa[1]	Himalaya andromeda	✔	✔		UK (outdoor and nursery)	Inman *et al.* (2003)
	Pieris japonica[1]	Japanese pieris	✔	✔		UK (nursery and outdoor), France (nursery), Germany (nursery and outdoor), Poland (nursery), USA (nursery)	CSL records, RAPRA (undated), Orlikowski & Szkuta (2004), Parke *et al.* (2004)
	Pieris japonica x *formosa*[1]	Ornamental pieris	✔	✔		UK (nursery), USA (nursery)	CSL records, Parke *et al.* (2004)

Family	Latin name	Common name	Damage type*			Location(s)†	References
			F	D	C		
	Rhododendron spp. [1]	Rhododendron	✔	✔		UK (nursery and outdoor), Belgium (nursery), Finland (nursery), France (nursery), Germany (nursery and outdoor), Ireland (nursery), Italy (nursery), the Netherlands (nursery and outdoor), Norway (outdoor), Poland (nursery), Slovenia (nursery), Spain (nursery), Sweden (nursery), Switzerland (nursery), Canada, (nursery), USA (nursery and outdoor)	CSL records, De Merlier *et al*. (2003), RAPRA (undated), Cahalane (2004), Gullino *et al*. (2003), de Gruyter & Steeghs (2006), Orlikowski & Szkuta (2002), Žerjav *et al*. (2004), Morajelo & Werres (2002), Goheen *et al*. (2002a), Anon. (2006a), COMTF (undated), Garbelotto *et al.* (2003)
	Vaccinium ovatum[1]	Californian huckleberry	✔	✔		USA (outdoor)	Garbelotto *et al.* (2003), Goheen *et al*. (2002a)
Fagaceae	*Castanea sativa*[1]	Sweet chestnut	✔	✔		UK (outdoor)	Denman *et al*. (2005)
	Castanopsis orthacantha	-	✔	✔		UK (outdoor)	Forest Research records
	Fagus sylvatica[1]	Beech			✔	UK (outdoor), Netherlands (outdoor)	Forest Research records, RAPRA (undated)
	Lithocarpus densiflorus[1]	Tanoak	✔	✔	✔	USA (outdoor)	Garbelotto *et al.* (2003)
	Nothofagus obliqua	Roble beech			✔	UK (outdoor)	Forest Research records
	Quercus acuta	Japanese evergreen oak			✔	UK (outdoor)	Forest Research records
	Quercus agrifolia[1]	Coast live oak			✔	USA (outdoor)	Garbelotto *et al.* (2003)
	Quercus chrysolepis[1]	Canyon live oak		✔	✔	USA (outdoor)	Murphy & Rizzo (2003)
	Quercus cerris[1]	Turkey oak	✔		✔	UK (outdoor)	Forest Research records
	Quercus falcata[1]	Southern red oak			✔	UK (outdoor)	Brasier *et al*. (2004a)
	Quercus ilex[1]	Holm oak	✔	✔		UK (outdoor)	Denman *et al*. (2005)
	Quercus kelloggii[1]	Californian black oak			✔	USA (outdoor)	Garbelotto *et al.* (2003)
	Quercus parvula var. *shrevei* [1]	Shreve oak			✔	USA (outdoor)	Garbelotto *et al.* (2003)
	Quercus petraea	Sessile oak			✔	UK (outdoor)	Forest Research records
	Quercus rubra	Northern red oak			✔	Netherlands (outdoor)	RAPRA (undated)
Garryaceae	*Garrya elliptica*	Silk tassel bush	✔			UK (nursery)	CSL records

Family	Latin name	Common name	Damage type*			Location(s)†	References
			F	D	C		
Hamamelidaceae	*Corylopsis spicata*	Spike winter hazel	✔			Canada (nursery)	CFIA records
	Distylium myricoides	Myrtle-leafed distylium	✔			Canada (nursery)	CFIA records
	Hamamelis mollis	Chinese witch hazel	✔	✔		UK (nursery)	CSL records
	Hamamelis virginiana[1]	Virginian witch hazel	✔	✔		UK (nursery and outdoor)	Giltrap *et al.* (2004)
	Hamamelis x *intermedia* (*H. mollis* x *H. japonica*)	Hybrid witch hazel	✔			Canada (nursery)	Anon. (2006a)
	Loropetalum chinense	Loropetalum	✔			Canada (nursery); USA (nursery),	APHIS records; COMTF (undated)
	Parrotia persica[1]	Ironwood	✔	✔		UK (outdoor), Canada (nursery)	Hughes *et al.* (2006b), CFIA records
Hippocastanaceae	*Aesculus californica*[1]	Californian buckeye	✔	✔		USA (outdoor)	Garbelotto *et al.* (2003)
	Aesculus hippocastanum[1]	Horse chestnut			✔	UK (outdoor)	Forest Research records
Lauraceae	*Cinnamomum* sp.[4]	-				Canada (nursery)	CFIA records
	Cinnamomum camphora	Camphor tree	✔	✔		UK (outdoor)	Forest Research records
	Laurus nobilis[1]	Bay laurel	✔			UK (nursery)	CSL records
	Umbellularia californica[1]	Californian bay laurel	✔			UK (outdoor), USA (outdoor)	CSL records, Garbelotto *et al.* (2003)
Liliaceae	*Clintonia andrewsiana*	Andrew's clintonia bead lily	✔			USA (outdoor)	COMTF (undated)
	Maianthemum racemosum [syn. *Smilacina racemosa*]	False Solomon's seal	✔			USA (outdoor)	COMTF (undated)
Magnoliaceae	*Magnolia denudata*	Lily Tree	✔			Canada (nursery); UK (outdoor)	CFIA records; FR records
	Magnolia grandiflora[1]	Magnolia	✔			UK (nursery and outdoor), USA (nursery), Canada (nursery)	CSL records, COMTF (undated)
	Magnolia kobus	Kobus magnolia	✔			Canada (nursery)	CFIA records
	Magnolia stellata[1]	Star magnolia	✔	✔		UK (nursery and outdoor)	Giltrap *et al.* (2006)
	Magnolia x *loebneri*[1] (*M. kobus* & *M. stellata*)	Loebner magnolia	✔	✔		UK (nursery and outdoor)	Giltrap *et al.* (2006)
	Magnolia salicifolia	Anise magnolia	✔			UK (outdoor)	Forest Research records

Family	Latin name	Common name	Damage type*			Location(s)†	References
			F	D	C		
Magnoliaceae (continued)	*Magnolia* x *soulangeana* (*M. liliiflora* x *M. denudate*)	Saucer magnolia	✔	✔		UK (nursery)	CSL records
	Magnolia denudata x *salicifolia*	Magnolia hybrid	✔			UK (outdoor)	Forest Research records
	Michelia cavalieri	Michelia	✔			Canada (nursery)	CFIA records
	Michelia doltsopa[1]	Michelia	✔			UK (outdoor)	Forest Research records
	Michelia foveolata	Michelia	✔			Canada (nursery)	CFIA records
	Michelia maudiae[1]	Michelia	✔			UK (outdoor), Canada (nursery)	CSL records, APHIS records
	Michelia wilsonii	Michelia	✔			Canada (nursery)	APHIS records
	Manglietia insignis	Red lotus tree	✔			Canada (nursery)	APHIS records
	Parakmeria lotungensis	Eastern joy lotus tree	✔			Canada (nursery)	APHIS records
Myrtaceae	*Eucalyptus haemastoma*	Scribbly gum	✔			UK (outdoor)	Forest Research records
Mysinaceae	*Ardisia japonica*	Japanese ardisia, Maleberry	✔			Canada (nursery)	COMTF (undated)
Oleaceae	*Fraxinus excelsior*[1]	Ash	✔			UK (outdoor)	Forest Research records
	Fraxinus latifolia	Oregon ash	✔			USA (outdoor)	COMTF (undated)
	Osmanthus heterophyllus[1]	Holly osmanthus	✔			UK (nursery), USA (nursery)	CSL records, COMTF (undated)
	Osmanthus decorus	Osmanthus	✔			Canada (nursery)	RAPRA (undated)
	Osmanthus delavayi	Delavay osmanthus	✔			USA (nursery), UK (outdoor)	COMTF (undated); Forest Research records
	Osmanthus fragrans	Sweet olive	✔	✔		USA (nursery), Canada (nursery)	COMTF (undated), CFIA records
	Syringa sp.	Not identified to species level				Canada (nursery)	CFIA records
	Syringa vulgaris[1]	Lilac	✔	✔		UK (outdoor and nursery)	Beales *et al.* (2004a)
Pinaceae	*Abies concolor*	White fir	✔			USA (outdoor)	COMTF (undated)
	Abies grandis	Grand fir	✔	✔		USA (outdoor)	COMTF (undated)
	Abies magnifica	Red fir	✔	✔		USA (outdoor)	COMTF (undated)
	Pseudotsuga menziesii[1]	Douglas fir	✔	✔		USA (outdoor)	Davidson *et al.* (2002)
Pittosporaceae	*Pittosporum undulatum*	Victorian box	✔			USA (outdoor)	Hüberli *et al.* (2006)

Family	Latin name	Common name	Damage type*			Location(s)†	References
			F	D	C		
Polypoidiaceae	*Adiantum aleuticum*[1] [syn. *Adiantum pedatum*]	Western maidenhair fern	✔			USA (outdoor)	Vettraino *et al.* (2006)
	Adiantum jordanii[1]	California maidenhair fern	✔			USA (outdoor)	COMTF (undated)
Primulaceae	*Trientalis latifolia*[1]	Western star flower	✔			USA (outdoor)	Hüberli *et al.* (2003)
Rhamnaceae	*Ceanothus thyrsiflorus*	Blue blossom, Californian lilac	✔	✔		USA (outdoor)	COMTF (undated)
	Frangula californica[1] [syn. *Rhamnus californica*]	Californian coffeeberry, California buckthorn	✔	✔		USA (outdoor)	Garbelotto *et al.* (2003)
	Frangula purshiana[1] [syn. *Rhamnus purshiana*]	Cascara	✔			USA (outdoor)	Vettraino *et al.* (2006), Goheen *et al.* (2002b)
Rosaceae	*Heteromeles arbutifolia*[1]	Toyon	✔	✔		USA (outdoor)	Garbelotto *et al.* (2003)
	Photinia x *fraseri*[1] (*P. glabra* x *P. serrulata*)	Fraser photinia	✔			Poland (outdoor)	Orlikowski & Szkuta (2004)
	Pyracantha koidzumii	Formosa firethorn	✔			Canada (nursery)	Briere *et al.* (2005)
	Prunus laurocerasus 'Nana'	Dwarf English Laurel	✔			USA (nursery)	COMTF (undated)
	Prunus lusitanica	Portuguese laurel cherry	✔			Canada (nursery)	COMTF (undated)
	Rosa spp. (several different cultivars)	Rose	✔			Canada (nursery)	APHIS records
	Rosa gymnocarpa[1]	Californian wood rose	✔			USA (outdoor)	Hüberli *et al.* (2004)
	Rosa rugosa	Rugosa rose	✔			Canada (nursery)	APHIS records
	Rubus spectabilis	Salmonberry	✔			USA (outdoor)	Goheen *et al.* (2002b)
Salicaceae	*Salix caprea*[1]	Goat willow/sallow	✔	✔		UK (nursery)[2]	CSL records
Taxaceae	*Taxus* sp.		✔			Canada (nursery)	CFIA records
	Taxus baccata[1]	Yew	✔	✔		UK (nursery)	Lane *et al.* (2004)
	Taxus brevifolia	Pacific yew	✔	✔	✔	USA (outdoor)	COMTF (undated)
	Taxus x *media* (*T. baccata* x *T. cuspidata*)	Anglojap yew			✔	Netherlands (nursery)	de Gruyter & Steeghs (2006)
	Torreya california	California nutmeg	✔	✔		USA (outdoor)	COMTF (undated)
Taxodiaceae	*Sequoia sempervirens*[1]	Coast redwood		✔	✔	USA (outdoor)	Maloney et al. (2002)

Family	Latin name	Common name	Damage type*			Location(s)†	References
			F	D	C		
Theacae	*Camellia* spp.[1]	Camellia	✔	✔		UK (nursery and outdoor), Spain (nursery), USA (nursery and outdoor), Canada (nursery)	Beales *et al*. (2004b), Pintos Varela *et al*. (2003), COMTF (undated), CFIA records
	Schima sp.[3]	-			✔	UK (outdoor)	Forest Research records
	Schima wallichii	Chinese guger tree	✔			UK (outdoor)	CSL records
Winteraceae	*Drimys winteri*	Winter's bark	✔	✔		UK (outdoor)	CSL records

Appendix 2. Species susceptibilities to *P. ramorum* as determined by experimental tests

Compiled from the RAPRA Database of potential hosts (as of 9th August 2006) http://rapra.csl.gov.uk

Host name	Common name	Host family	Test method	Wounded?	Plant part tested	Symptom	Susceptibility*	Reference
Abies concolor	White fir	Pinaceae	Stem susceptibility by wound inoculation with mycelial plugs	Yes	Stem	Details not supplied	Ms	Hansen *et al*., 2005
Abies grandis	Grand fir	Pinaceae	Log inoculations	Yes	Inner bark	Inner bark death and bleeding cankers	Ms	Brasier *et al*., *Personal Communication*
Abies grandis	Grand fir	Pinaceae	Leaf dip in zoospore suspension	No	Leaf	Details not supplied	Ms	Hansen *et al*., 2005
Abies grandis	Grand fir	Pinaceae	Stem susceptibility by wound inoculation with mycelial plugs	Yes	Stem	Details not supplied	Ls	Hansen *et al*., 2005
Abies grandis	Grand fir	Pinaceae	Whole plant dip in zoospore suspension	No	Whole plant	Details not supplied	Ms	Hansen *et al*., 2005
Abies magnifica	Red fir	Pinaceae	Stem susceptibility by wound inoculation with mycelial plugs	Yes	Stem	Details not supplied	Ms	Hansen *et al*., 2005
Abies magnifica	Red fir	Pinaceae	Whole plant dip in zoospore suspension	No	Whole plant	Details not supplied	R	Hansen *et al*., 2005
Abies procera	Noble Fir	Pinaceae	Sapling stem inoculation	Yes	Stem	Stem lesion	Ms	Denman *et al*., *Personal Communication*
Abies procera	Noble fir	Pinaceae	Detached leaves dipped in zoospore suspensions	No	Leaf	Needles showing necrosis	Hs	Denman *et al*., 2005
Abies procera	Noble fir	Pinaceae	Log inoculations	Yes	Inner bark	Inner bark death and bleeding cankers	Ls	Brasier *et al*., *Personal Communication*
Abies procera	Noble fir	Pinaceae	Stem susceptibility by wound inoculation with mycelial plugs	Yes	Stem	Details not supplied	Ms	Hansen *et al*., 2005
Abies procera	Noble fir	Pinaceae	Whole plant dip in zoospore suspension	No	Whole plant	Details not supplied	R	Hansen *et al*., 2005
Abies procera	Noble fir	Pinaceae	Leaf dip in zoospore suspension	No	Leaf	Details not supplied	Hs	Hansen *et al*., 2005
Acer campestre	Field maple	Aceraceae	Wounded stem tests using mycelial plugs	Yes	Stem	Bark necrosis	Hs	Vannini, *Personal Communication*
Acer campestre	Field maple	Aceraceae	Detached leaf dip in zoospore suspension	No	Leaf	Foliar necrosis	Ls	Vannini, *Personal Communication*
Acer campestre	Field maple	Aceraceae	Zoospore suspension dipping	No	Stem/Leaf	Lesion not extending much beyond wound	R	Defra, PH0193S
Acer campestre	Field maple	Aceraceae	Mycelial plug inoculum on leaf	Yes	Leaf	Lesion not extending much beyond wound	R	Defra, PH0193S
Acer circinatum	Vine maple	Aceraceae	Details not supplied	Yes	Stem	Details not supplied	Ls	Hansen *et al*., 2005

* R, resistance; Ls, low susceptibility; Ms, Moderate susceptibility; Hs, High susceptibility. Note that susceptibilities are from many different experiments and care should be applied with regard to direct comparisons between different pieces of work.

Host name	Common name	Host family	Test method	Wounded?	Plant part tested	Symptom	Susceptibility*	Reference
Acer circinatum	Vine maple	Aceraceae	Whole plant dip in zoospore suspension	No	Whole plant	Details not supplied	R	Hansen *et al*., 2005
Acer circinatum	Vine maple	Aceraceae	Leaf dip in zoospore suspension	No	Leaf	Details not supplied	Ls - R	Hansen *et al*., 2005
Acer macrophyllum	Bigleaf maple	Aceraceae	Stem susceptibility by wound inoculation with mycelial plugs	Yes	Stem	Details not supplied	Ms	Hansen *et al*., 2005
Acer macrophyllum	Bigleaf maple	Aceraceae	Leaf inoculation by pinning a mycelial plug to the upper surface of leaves	Yes	Leaf	Leaf lesions	Ms	Garbelotto *et al*., 2003
Acer macrophyllum	Bigleaf maple	Aceraceae	Whole plant dip in zoospore suspension	No	Whole plant	Details not supplied	R	Hansen *et al*., 2005
Acer macrophyllum	Bigleaf maple	Aceraceae	Log inoculations	Details not supplied	Inner bark	Details not supplied	Ls	Hansen *et al*., 2005
Acer macrophyllum	Bigleaf maple	Aceraceae	Leaf dip in zoospore suspension	No	Leaf	Details not supplied	Ms	Hansen *et al*., 2005
Acer monspessulanum	Montpellier maple	Aceraceae	Wounded stem tests using mycelial plugs	Yes	Stem	Bark necrosis	Ls	Vannini, *Personal Communication*
Acer monspessulanum	Montpellier maple	Aceraceae	Detached leaf dip in zoospore suspension	No	Leaf	Foliar necrosis	Ls	Vannini, *Personal Communication*
Acer monspessulanum	Montpellier maple	Aceraceae	Zoospore point inoculation	Yes	Detached leaf	Leaf necrosis	Ls	Moralejo *et al*., *Personal Communication*
Acer monspessulanum	Montpellier maple	Aceraceae	Log inoculation	Yes	Inner bark	Inner bark necrosis	Ls	Moralejo *et al*., *Personal Communication*
Acer palmatum	Japanese maple	Aceraceae	Detached leaf dip in zoospore suspension	No	Leaf	Foliar necrosis	Hs	Parke *et al*., 2002a
Acer platanoides	Norway maple	Aceraceae	Detached leaf dip in zoospore suspension	No	Leaf	Foliar necrosis	Ls	Vannini, *Personal Communication*
Acer platanoides	Norway maple	Aceraceae	Wounded stem tests using mycelial plugs	Yes	Stem	Bark necrosis	Ms	Vannini, *Personal Communication*
Acer pseudoplatanus	Sycamore	Aceraceae	Detached leaves dipped in zoospore suspensions	No	Leaf	Low proportion with necrosis, high level of back isolation	Ls	Denman *et al*., 2005
Acer pseudoplatanus	Sycamore	Aceraceae	Mycelial plug inoculum on leaf	Yes	Leaf	Lesion extension slight	Ls	Defra, PH0193S
Acer pseudoplatanus	Sycamore	Aceraceae	Stem susceptibility by wound inoculation with mycelial plugs	Yes	Stem	Lesion extension slight	Ls	Defra, PH0193S
Acer pseudoplatanus	Sycamore	Aceraceae	Zoospore suspension dipping	No	Stem/Leaf	Lesion extension slight	Ls	Defra, PH0193S
Acer pseudoplatanus	Sycamore	Aceraceae	Log inoculations	Yes	Inner bark	Inner bark death and bleeding cankers	Ls	Brasier *et al*., 2002
Acer sp.	Maple	Aceraceae	Details not supplied	Details not supplied	Details not supplied	Details not supplied	Ls	Inman *et al*., 2002
Aesculus californica	California buckeye	Hippocastanaceae	Leaf inoculation by pinning a mycelial plug to the upper surface of leaves	Yes	Leaf	Leaf lesions	Ms	Garbelotto *et al*., 2003
Aesculus hippocastanum	Horse chestnut	Hippocastanaceae	Detached leaves dipped in zoospore suspensions	No	Leaf	High proportion with necrosis, high level of back isolation	Hs - Ms	Denman *et al*., 2005

Host name	Common name	Host family	Test method	Wounded?	Plant part tested	Symptom	Susceptibility*	Reference
Aesculus hippocastanum	Horse chestnut	Hippocastanaceae	Log inoculations	Yes	Inner bark	Inner bark death and bleeding cankers	Ls	Brasier *et al*., 2002
Alnus glutinosa	Alder	Betulaceae	Wounded stem tests using mycelial plugs	Yes	Stem	Bark necrosis	Ls	Vannini, *Personal Communication*
Alnus glutinosa	Alder	Betulaceae	Detached leaf dip in zoospore suspension	No	Leaf	Foliar necrosis	Ls	Vannini, *Personal Communication*
Alnus glutinosa	European alder, black alder	Betulaceae	Mycelial plug inoculum on leaf	Yes	Leaf	Lesion not extending much beyond wound	R	Defra, PH0193S
Alnus glutinosa	European alder, black alder	Betulaceae	Log inoculations	Yes	Inner bark	Inner bark death and bleeding cankers	Ls	Brasier *et al*., *Personal Communication*
Alnus glutinosa	European alder, black alder	Betulaceae	Detached leaves dipped in zoospore suspensions	No	Leaf	Low proportion with necrosis, low level of back isolation	Ls	Denman *et al*., 2005
Alnus incana	Gray alder	Betulaceae	Wounded stem tests using mycelial plugs	Yes	Stem	Bark necrosis	Ls	Vannini, *Personal Communication*
Alnus rhombifolia	White alder	Betulaceae	Leaf dip in zoospore suspension	No	Leaf	Details not supplied	Ms	Hansen *et al*., 2005
Alnus rhombifolia	White alder	Betulaceae	Stem susceptibility by wound inoculation with mycelial plugs	Yes	Stem	Details not supplied	R	Hansen *et al*., 2005
Alnus rhombifolia	White alder	Betulaceae	Whole plant dip in zoospore suspension	No	Whole plant	Details not supplied	Ls	Hansen *et al*., 2005
Alnus rubra	Red alder	Betulaceae	Whole plant dip in zoospore suspension	No	Whole plant	Details not supplied	R	Hansen *et al*., 2005
Alnus rubra	Red alder	Betulaceae	Stem susceptibility by wound inoculation with mycelial plugs	Yes	Stem	Details not supplied	Ls	Hansen *et al*., 2005
Alnus rubra	Red alder	Betulaceae	Detached leaf dip in zoospore suspension	No	Leaf	Details not supplied	Ls	Hansen *et al*., 2005
Alnus rubra	Red alder	Betulaceae	Log inoculations	Details not supplied	Inner bark	Details not supplied	Ls - Ms	Hansen *et al*., 2005
Alnus sp.	Alder	Betulaceae	Leaf inoculation	Details not supplied	Leaf	Details not supplied	R	Inman *et al*., 2002
Andromeda polifolia	Bog rosemary	Ericaceae	Details not supplied	Details not supplied	Leaves and stems	Stem lesions	Ls	Orlikowski & Szkuta, 2003
Andromeda polifolia	Bog rosemary	Ericaceae	Details not supplied	Details not supplied	Leaves and stems	Leaf necrosis	R	Orlikowski & Szkuta, 2003
Arbutus canariensis	Canary madrone	Ericaceae	Mycelial plug inoculum on leaf	Yes	Detached leaf	Leaf necrosis	Ms	Moralejo *et al*., *Personal Communication*
Arbutus menziesii	Madrone	Ericaceae	Leaf inoculation by pinning a mycelial plug to the upper surface of leaves	Yes	Leaf	Leaf lesions	Hs	Garbelotto *et al*., 2003
Arbutus unedo	Strawberry Tree	Ericaceae	Detached leaf dip in zoospore suspension	No	Leaf	Foliar necrosis	Ms	Vannini, *Personal Communication*
Arbutus unedo	Strawberry tree	Ericaceae	Zoospore point inoculation	Yes	Detached leaf	Leaf necrosis	Ls	Moralejo et al., *Personal Communication*

Host name	Common name	Host family	Test method	Wounded?	Plant part tested	Symptom	Susceptibility*	Reference
Arbutus unedo	Strawberry tree	Ericaceae	Detached leaf dip in zoospore suspension	No	Leaf	Necrotic lesions followed by extensive blight.	Ms - Hs	Moralejo & Hernandez, 2002
Arbutus unedo	Strawberry tree	Ericaceae	Mycelial plug on twig	Yes	Twig cutting	Blight	Ms	Moralejo *et al*., *Personal Communication*
Arbutus unedo	Strawberry tree	Ericaceae	Log inoculation	Yes	Inner bark	inner bark necrosis	Ms	Moralejo *et al*., *Personal Communication*
Arbutus xalapensis	Madrone	Ericaceae	Whole plant dip in zoospore suspension	No	Whole plant	Dieback	Hs	Hansen *et al*., 2005
Arbutus xalapensis	Madrone	Ericaceae	Log inoculations	Details not supplied	Inner bark	Details not supplied	Ls - R	Hansen *et al*., 2005
Arbutus xalapensis	Madrone	Ericaceae	Leaf dip in zoospore suspension	No	Leaf	Details not supplied	Hs	Hansen *et al*., 2005
Arbutus xalapensis	Madrone	Ericaceae	Stem susceptibility by wound inoculation with mycelial plugs	Yes	Stem	Girdled	Hs	Hansen *et al*., 2005
Arctostaphylos manzanita	Manzanita	Ericaceae	Leaf inoculation by pinning a mycelial plug to the upper surface of leaves	Yes	Leaf	Leaf lesions	Ms	Garbelotto *et al*., 2003
Arctostaphylos uva-ursi	Bearberry	Ericaceae	Heathland species also tested by zoospore suspension dipping	No	Leaf	Lesion well developed	Ms	Defra, PH0193S
Arctostaphylos uva-ursi	Bearberry	Ericaceae	Mycelial plug inoculum on leaf	Yes	Leaf	Lesion well developed	Ms	Defra, PH0193S
Arctostaphylos uva-ursi	Bearberry	Ericaceae	Detached leaf dip in zoospore suspension	Details not supplied	Leaf	Details not supplied	Ms	Tooley & Englander, 2002
Aucuba japonica	Japanese laurel	Aucubaceae	Mycelial plug inoculum on leaf	Yes	Leaf	No necrosis or necrosis only in damaged tissue	Virtually immune	Defra, PH0193S
Betula pendula	European white birch, Silver birch	Betulaceae	Detached leaves dipped in zoospore suspensions	No	Leaf	Low proportion with leaf necrosis, low level of back isolation	Ls	Denman *et al*., 2005
Betula pendula	European white birch, Silver birch	Betulaceae	Log inoculations	Yes	Inner bark	Inner bark death and bleeding cankers	Ls	Brasier *et al*., *Personal Communication*
Buddleja davidii	Butterfly bush, Summer lilac	Loganiaceae	Mycelial plug inoculum on leaf	Yes	Leaf	No necrosis or necrosis only in damaged tissue	Virtually immune	Defra, PH0193S
Buddleja davidii	Butterfly bush, Summer lilac	Loganiaceae	Detached leaf dip in zoospore suspension	No	Leaf	Foliar necrosis	Hs	Parke *et al*., 2002a
Calluna vulgaris	Heather	Ericaceae	Dipped in zoospore suspension	No	Shoots with leaves	Shoot necrosis	Hs	Wagner *et al*., 2005
Calluna vulgaris	Heather	Ericaceae	Details not supplied	Details not supplied	Stems	Stem lesions	Ms	Orlikowski & Szkuta, 2003
Calluna vulgaris	Heather	Ericaceae	Mycelial discs on wounded petioles, stem bases or shoots	Yes	Petioles, stem bases, shoots	Details not supplied	Not given	Orlikowski & Szkuta, 2002
Calluna vulgaris	Heather	Ericaceae	Mycelial plugs	Details not supplied	Apical tip of shoots	Necrosis	Ms	Orlikowski & Szkuta, 2004
Calluna vulgaris	Heather	Ericaceae	Unwounded and wounded; zoospore suspension dipping	Yes and No	Leaves and stems	Leaf necrosis	Hs	Defra, PH0193S
Calluna vulgaris 'Winter chocolate'	Heather	Ericaceae	Unwounded and wounded; zoospore suspension dipping	Yes and No	Leaves and stems	Leaf necrosis	Hs	Defra, PH0193S

Host name	Common name	Host family	Test method	Wounded?	Plant part tested	Symptom	Susceptibility*	Reference
Calocedrus decurrens	Incense cedar	Cupressaceae	Whole plant dip in zoospore suspension	No	Whole plant	Details not supplied	R	Hansen *et al*., 2005
Calocedrus decurrens	Incense cedar	Cupressaceae	Stem susceptibility by wound inoculation with mycelial plugs	Yes	Stem	Details not supplied	R	Hansen *et al*., 2005
Camellia japonica	Common camellia	Ericaceae	Detached foliage dipped into a suspension of mycelial fragments and sporangia	No	Leaf	Leaf necrosis, petiole lesions	Ms	Orlikowski & Szkuta, 2003
Camellia japonica	Common camellia	Ericaceae	Mycelial plug inoculum on leaf	Yes	Leaf	Lesions very extensive	Hs	Defra, PH0193S
Camellia japonica	Common camellia	Ericaceae	Zoospore suspension dipping	No	Stem/Leaf	Lesions very extensive	Hs	Defra, PH0193S
Camellia japonica	Common camellia	Ericaceae	Stem susceptibility by wound inoculation with mycelial plugs	Yes	Stem	Lesions very extensive	Hs	Defra, PH0193S
Camellia japonica	Common camellia	Ericaceae	Detached leaf dip in zoospore suspension	Details not supplied	Leaf	Details not supplied	R	Linderman *et al*., 2002
Camellia japonica	Common camellia	Ericaceae	Detached foliage dipped in zoospore suspension	No	Leaf	Leaf and petiole necrosis	Ms	Pintos Varela *et al*., 2003
Camellia sasanqua	Sasanqua Camellia	Theaceae	Mycelial plugs	Yes	Leaf	Foliage with necrosis, bud and stem death, necrotic lesions, leaf abscission	Ms	Parke *et al*., 2004
Camellia sp.	Camellia	Ericaceae	Leaf inoculation	Details not supplied	Leaf	Details not supplied	Hs	Inman *et al*., 2002
Camellia sp.	Camellia	Ericaceae	Not reported	Details not supplied	Detached leaf	Leaf necrosis (blight)	Not rated, just given as susceptible	Beales *et al*., 2004a
Carpinus betulus	Hornbeam	Betulaceae	Log inoculations	Yes	Inner bark	Inner bark death and bleeding cankers	R	Brasier *et al*., *Personal Communication*
Carpinus betulus	Hornbeam	Betulaceae	Detached leaves dipped in zoospore suspensions	No	Leaf	Low proportion with leaf necrosis, high level of back isolation	Ls	Denman *et al*., 2005
Castanea sativa	Sweet chestnut	Fagaceae	Zoospore point inoculation	Yes	Detached leaf	Leaf necrosis	Ls	Moralejo *et al*., *Personal Communication*
Castanea sativa	Sweet chestnut	Fagaceae	Log inoculations	Yes	Inner bark	Inner bark death and bleeding cankers	More susceptible	Brasier *et al*., *Personal Communication*
Castanea sativa	Sweet chestnut	Fagaceae	Sapling stem inoculation	Yes	Stem	Stem lesion	Hs	Denman *et al*., *Personal Communication*
Castanea sativa	Sweet chestnut	Fagaceae	Detached leaves dipped in zoospore suspensions	No	Leaf	High proportion with leaf necrosis, high level of back isolation	Ms	Denman *et al*., 2005
Castanopsis chryophylla	Giant chinquapin, Giant chinkapin, Golden chinkapin	Fagaceae	Log inoculations	Yes	Inner bark	Inner bark necrosis	Ls - Hs	Hansen *et al*., 2005
Ceanothus impressus	Californian lilac, Santa Barbara	Rhamnaceae	Detached leaf dip in zoospore suspension	No	Leaf	Foliar necrosis	Hs	Parke *et al*., 2002a
Celtis australis	Netle tree	Ulmaceae	Mycelial plug inoculum on leaf	Yes	Detached leaf	Leaf necrosis	Ms - Hs	Moralejo *et al*., *Personal Communication*

Host name	Common name	Host family	Test method	Wounded?	Plant part tested	Symptom	Susceptibility*	Reference
Ceratonia siliqua	Carob, St. John's Bread	Leguminosae	Wounded stem tests using mycelial plugs	Yes	Stem	Bark necrosis	Ls	Vannini, *Personal Communication*
Ceratonia siliqua	Carob, St. John's Bread	Leguminosae	Detached leaf dip in zoospore suspension	No	Leaf	Foliar necrosis	Ls	Vannini, *Personal Communication*
Ceratonia siliqua	Carob, St. John's Bread	Leguminosae	Mycelial plug inoculum on leaf	Yes	Detached leaf	Leaf necrosis	Ls - Ms	Moralejo *et al*., *Personal Communication*
Ceratonia siliqua	Carob, St. John's Bread	Leguminosae	Detached leaf dip in zoospore suspension	No	Leaf	Necrotic lesions followed by extensive blight.	Hs	Moralejo & Hernandez, 2002
Ceratonia siliqua	Carob, St. John's Bread	Leguminosae	Mycelial plug on twig	Yes	Twig cutting	Bark necrosis	Ls	Moralejo *et al*., *Personal Communication*
Cercis siliquastrum	Judas tree	Leguminosae	Detached leaf dip in zoospore suspension	No	Leaf	Foliar necrosis	Hs	Vannini, *Personal Communication*
Cercis siliquastrum	Judas tree	Leguminosae	Wounded stem tests using mycelial plugs	Yes	Stem	Bark necrosis	Ls	Vannini, *Personal Communication*
Chaenomeles speciosa	Flowering quince	Rosaceae	Detached leaf dip in zoospore suspension	No	Leaf	No symptoms were observed	R	Parke *et al*., 2002a
Chamaecyparis lawsoniana	Port-Orford cedar, Lawson's cypress	Pinaceae	Log inoculations	Yes	Inner bark	Inner bark death and bleeding cankers	More susceptible	Brasier *et al*., *Personal Communication*
Chamaecyparis lawsoniana	Port-Orford cedar, Lawson's cypress	Pinaceae	Detached leaf dip in zoospore suspension	Details not supplied	Leaf	Details not supplied	Ms	Zanzot *et al*., 2002
Chamaecyparis lawsoniana	Port-Orford cedar, Lawson's cypress	Pinaceae	Detached leaves dipped in zoospore suspensions	No	Leaf	Needles generally unaffected	R	Denman *et al*., 2005
Chamaecyparis lawsoniana	Lawsons cypress	Pinaceae	Sapling stem inoculation	Yes	Stem	Stem lesion	Ls	Denman *et al*., *Personal Communication*
Chamaecyparis lawsoniana	Port-Orford cedar, Lawson's cypress	Pinaceae	Log inoculations	Details not supplied	Inner bark	Details not supplied	Ms	Hansen *et al*., 2005
Chamaecyparis lawsoniana	Port-Orford cedar, Lawson's cypress	Pinaceae	Log inoculations	Yes	Inner bark	Inner bark necrosis	Ls - Ms	Hansen *et al*., 2005
Chamaecyparis lawsoniana	Port-Orford cedar, Lawson's cypress	Pinaceae	Stem susceptibility by wound inoculation with mycelial plugs	Yes	Stem	Details not supplied	R	Hansen *et al*., 2005
Chamaecyparis lawsoniana	Port-Orford cedar, Lawson's cypress	Pinaceae	Whole plant dip in zoospore suspension	No	Whole plant	Details not supplied	R	Hansen *et al*., 2005
Chamaecyparis lawsoniana	Port-Orford cedar, Lawson's cypress	Pinaceae	Leaf dip in zoospore suspension	No	Leaf	Details not supplied	R	Hansen *et al*., 2005
Choisya ternata	Mexican orange blossom	Rutaceae	Mycelial plug inoculum on leaf	Yes	Leaf	No necrosis or necrosis only in damaged tissue	Virtually immune	Defra, PH0193S
Chrysolepis chrysophlla	Golden chinquapin	Fagaceae	Log inoculations	Details not supplied	Inner bark	Details not supplied	Hs	Hansen *et al*., 2005
Chrysolepis chrysophlla	Golden chinquapin	Fagaceae	Stem susceptibility by wound inoculation with mycelial plugs	Yes	Stem	Details not supplied	Ms	Hansen *et al*., 2005
Cistus salviifolius	Rock rose	Cistaceae	Detached leaf dip in zoospore suspension	No	Leaf	Details not supplied	Ms	Moralejo & Hernandez, 2002
Cistus salviifolius	Rock rose	Cistaceae	Zoospore point inoculation	Yes	Detached leaf	Leaf necrosis	Ls - Ms	Moralejo *et al*., *Personal Communication*

Host name	Common name	Host family	Test method	Wounded?	Plant part tested	Symptom	Susceptibility*	Reference
Citrus deliciosa	Tangerine	Rutaceae	Mycelial plug inoculum on leaf	Yes	Detached leaf	Leaf necrosis	Ls - Ms	Moralejo *et al*., *Personal Communication*
Citrus limon	Lemon tree	Rutaceae	Mycelial plug inoculum on leaf	Yes	Detached leaf	Leaf necrosis	Ls	Moralejo *et al*., *Personal Communication*
Citrus sinensis	Orange tree	Rutaceae	Zoospore point inoculation	No	Detached leaf	Details not supplied	R	Moralejo *et al*., *Personal Communication*
Clematis flammula	Fragrant virgin's bower	Ranunculaceae	Detached leaf dip in zoospore suspension	No	Leaf	Details not supplied	Ms	Moralejo & Hernandez, 2002
Clematis montana	Anenome clematis	Ranunculaceae	Mycelial plug inoculum on leaf	Yes	Leaf	Lesion not extending much beyond wound	R	Defra, PH0193S
Clematis montana	Anenome clematis	Ranunculaceae	Detached leaf dip in zoospore suspension	No	Leaf	Foliar necrosis	Hs	Parke *et al*., 2002a
Cornus alba	Tatarian dogwood	Cornaceae	Mycelial plug inoculum on leaf	Yes	Leaf	Lesion not extending much beyond wound	R	Defra, PH0193S
Cornus florida	Flowering dogwood	Cornaceae	Detached leaf dip in zoospore suspension	No	Leaf	No symptoms were observed	Not given	Parke *et al*., 2002a
Cornus mas	Cornelian cherry	Cornaceae	Wounded stem tests using mycelial plugs	Yes	Stem	Bark necrosis	Ms	Vannini, *Personal Communication*
Cornus mas	Cornelian cherry	Cornaceae	Detached leaf dip in zoospore suspension	No	Leaf	Foliar necrosis	Ls	Vannini, *Personal Communication*
Cornus nuttalii	Pacific dogwood	Cornaceae	Leaf dip in zoospore suspension	No	Leaf	Details not supplied	Hs	Hansen *et al*., 2005
Cornus nuttalii	Pacific dogwood	Cornaceae	Whole plant dip in zoospore suspension	No	Whole plant	Details not supplied	Ms	Hansen *et al*., 2005
Cornus nuttalii	Pacific dogwood	Cornaceae	Stem susceptibility by wound inoculation with mycelial plugs	Yes	Stem	Details not supplied	Ls	Hansen *et al*., 2005
Cornus sanguinea	Dogwood	Cornaceae	Detached leaf dip in zoospore suspension	No	Leaf	Foliar necrosis	Ls	Vannini, *Personal Communication*
Corylus	Hazel	Betulaceae	Zoospore point inoculation	Yes	Detached leaf	Leaf necrosis	Ls	Moralejo *et al*., *Personal Communication*
Corylus americana	Hazel	Betulaceae	Leaf dip in zoospore suspension	No	Leaf	Details not supplied	Ms	Hansen *et al*., 2005
Corylus avellana	Hazel	Betulaceae	Log inoculation	Yes	Inner bark	Inner bark necrosis	Ls	Moralejo *et al*., *Personal Communication*
Corylus avellana	Hazel	Corylaceae	Detached leaves dipped in zoospore suspensions	No	Leaf	Low proportion with leaf necrosis, low level of back isolation	R	Denman *et al*., 2005
Corylus avellana	Hazel	Betulaceae	Mycelial plug inoculum on leaf	Yes	Leaf	Lesion not extending much beyond wound	R	Defra, PH0193S
Corylus avellana	Hazel	Corylaceae	Detached leaf dip in zoospore suspension	No	Leaf	Details not supplied	Ms	Hansen *et al*., 2005
Corylus avellana	Hazel	Corylaceae	Stem susceptibility by wound inoculation with mycelial plugs	Yes	Stem	Details not supplied	R	Hansen *et al*., 2005
Corylus avellana	Hazel	Corylaceae	Whole plant dip in zoospore suspension	No	Whole plant	Details not supplied	Ls	Hansen *et al*., 2005

Host name	Common name	Host family	Test method	Wounded?	Plant part tested	Symptom	Susceptibility*	Reference
Corylus sp.	Hazel	Corylaceae	Leaf inoculation	Details not supplied	Leaf	Details not supplied	R	Inman *et al*., 2002
Cotoneaster multiflorus	Cotoneaster	Rosaceae	Detached leaf dip in zoospore suspension	No	Leaf	No symptoms were observed	Not given	Parke *et al*., 2002a
Crataegus monogyna	Hawthorn	Rosaceae	Detached leaf dip in zoospore suspension	No	Leaf	Foliar necrosis	Ls	Vannini, *Personal Communication*
Crataegus monogyna	Hawthorn	Rosaceae	Zoospore point inoculation	Yes	Detached leaf	Leaf necrosis	Ls	Moralejo *et al*., *Personal Communication*
Crataegus monogyna	Hawthorn	Rosaceae	Mycelial plug inoculum on leaf	Yes	Leaf	Lesion not extending much beyond wound	R	Defra, PH0193S
Cupressus sempervirens	Italian cypress	Cupressaceae	Log inoculation	Yes	Inner bark	Inner bark necrosis	R	Moralejo *et al*., *Personal Communication*
Daphne gnidium	Spurge flax	Thymelaeaceae	Zoospore point inoculation	Yes	Detached leaf	Leaf necrosis	Ms	Moralejo *et al*., *Personal Communication*
Empetrum nigrum	Heather	Ericaceae	Unwounded and wounded; zoospore suspension dipping	Yes and No	Leaves and stems	No necrosis	R	Defra, PH0193S
Erica arborea	Tree heath	Ericaceae	Zoospore point inoculation	Yes	Detached leaf	Leaf necrosis	Hs	Moralejo *et al*., *Personal Communication*
Erica carnea 'Snowstorm'	Heather	Ericaceae	Unwounded and wounded; zoospore suspension dipping	Yes and No	Leaves and stems	Leaf necrosis	Ls	Defra, PH0193S
Erica cinerea 'Glen Cairn'	Heather	Ericaceae	Unwounded and wounded; zoospore suspension dipping	Yes and No	Leaves and stems	Stem and flower necrosis	Ms	Defra, PH0193S
Erica gracilis	Heather	Ericaceae	Dipped in zoospore suspension	No	Shoots with leaves	Shoot necrosis	Hs	Wagner *et al*., 2005
Erica multiflora	Heather	Ericaceae	Zoospore point inoculation	Yes	Detached leaf	Leaf necrosis	Hs	Moralejo *et al*., *Personal Communication*
Erica tetralix	Heather	Ericaceae	Unwounded and wounded; zoospore dipping	Yes and No	Leaves and stems	No necrosis	R	Defra, PH0193S
Erica vagans 'Valerie Proudley'	Heather	Ericaceae	Unwounded and wounded; zoospore dipping	Yes and No	Leaves and stems	Leaf necrosis	Ls	Defra, PH0193S
Eucalyptus gunii	Cider gum tree	Myrtaceae	Detached leaves dipped in zoospore suspensions	Non-wound	Leaf	High proportion with necrosis, high level of back isolation	Ms	Denman *et al*., 2005
Eucalyptus sp.	Eucalyptus, Gum tree	Myrtaceae	Log inoculations	Yes	Inner bark	Inner bark death and bleeding cankers	Ls	Brasier *et al*., *Personal Communication*
Eucalyptus sp.	Eucalyptus, Gum tree	Myrtaceae	Mycelial plug inoculum on leaf	Yes	Leaf	Lesions very extensive	Hs	Defra, PH0193S
Euonymus japonicus	Japanese euonymus	Celastraceae	Mycelial plug inoculum on leaf	Yes	Detached leaf	Leaf necrosis	Hs	Moralejo *et al*., *Personal Communication*
Fagus sylvatica	Beech	Fagaceae	Mycelial plug on wounded stem	Yes	Stem	Severe twig dieback	Ms	de Gruyter *et al*., 2002
Fagus sylvatica	Beech	Fagaceae	Details not supplied	Details not supplied	Stems	Stem lesions	Ms	Orlikowski & Szkuta, 2003
Fagus sylvatica	Beech	Fagaceae	Detached leaves dipped in zoospore suspensions	No	Leaf	Low proportion with necrosis, low level of back isolation	R	Denman *et al*., 2005

Host name	Common name	Host family	Test method	Wounded?	Plant part tested	Symptom	Susceptibility*	Reference
Fagus sylvatica	Beech	Fagaceae	Log inoculations	Yes	Inner bark	Inner bark death and bleeding cankers	Ms	Brasier *et al*., *Personal Communication*
Fagus sylvatica	Beech	Fagaceae	Sapling stem inoculation	Yes	Stem	Stem lesion	Hs	Denman *et al*., *Personal Communication*
Fagus sylvatica	Beech	Fagaceae	Mycelial plug inoculum on leaf	Yes	Leaf	Lesion not extending much beyond wound	R	Defra, PH0193S
Forsythia sp.	Golden bells	Oleaceae	Mycelial plug inoculum on leaf	Yes	Leaf	No necrosis or necrosis only in damaged tissue	Virtually immune	Defra, PH0193S
Fraxinus angustifolia	Narrow leaved ash	Oleaceae	Log inoculation	Yes	Inner bark	Details not supplied	R	Moralejo *et al*. *Personal Communication*
Fraxinus angustifolia	Narrow leaved ash	Oleaceae	Mycelial plug inoculum on leaf	Yes	Detached leaf	Leaf necrosis	Hs	Moralejo *et al*. *Personal Communication*
Fraxinus excelsior	Ash	Oleaceae	Detached leaf dip in zoospore suspension	No	Leaf	Foliar necrosis	Ls	Vannini, *Personal Communication*
Fraxinus excelsior	Common ash, European ash	Oleaceae	Log inoculations	Yes	Inner bark	Inner bark death and bleeding cankers	R	Brasier *et al*., *Personal Communication*
Fraxinus excelsior	Common ash, European ash	Oleaceae	Detached leaves dipped in zoospore suspensions	No	Leaf	High proportion with necrosis, high level of back isolation	Hs	Denman *et al*., 2005
Fraxinus excelsior	Common ash, European ash	Oleaceae	Mycelial plug inoculum on leaf	Yes	Leaf	Lesion well developed	Ms	Defra, PH0193S
Fraxinus excelsior	Common ash, European ash	Oleaceae	Zoospore suspension dipping	No	Stem/Leaf	Lesion well developed	Ms	Defra, PH0193S
Fraxinus excelsior	Common ash, European ash	Oleaceae	Stem susceptibility by wound inoculation with mycelial plugs	Yes	Stem	Lesion well developed	Ms	Defra, PH0193S
Fraxinus latifolia	Oregon ash	Oleaceae	Leaf dip in zoospore suspension	No	Leaf	Details not supplied	Ms	Hansen *et al*., 2005
Fraxinus latifolia	Oregon ash	Oleaceae	Whole plant dip in zoospore suspension	No	Whole plant	Details not supplied	Ms - Ls	Hansen *et al*., 2005
Fraxinus latifolia	Oregon ash	Oleaceae	Stem susceptibility by wound inoculation with mycelial plugs	Yes	Stem	Details not supplied	R	Hansen *et al*., 2005
Fraxinus ornus	Flowering ash	Oleaceae	Detached leaf dip in zoospore suspension	No	Leaf	Foliar necrosis	Ls	Vannini, *Personal Communication*
Fuchsia sp.	Fuschia	Onagraceae	Mycelial plug inoculum on leaf	Yes	Leaf	Lesion well developed	Ms	Defra, PH0193S
Gaultheria shallon	Salal	Ericaceae	Detached leaf dip in zoospore suspension	Details not supplied	Leaf	Details not supplied	R	Linderman *et al*., 2002
Gaultheria sp.	Wintergreen	Ericaceae	Details not supplied	Details not supplied		Details not supplied	Ls	Inman *et al*., 2002
Gaultheria x *wisleyensis*	Wisley Pearl	Ericaceae	Mycelial plug inoculum on leaf	Yes	Leaf	Lesion extension slight	Ls	Defra, PH0193S
Gleditsia triacanthos	Honeylocust	Fabaceae	Detached leaf dip in zoospore suspension	No	Leaf	Foliar necrosis	Hs	Parke *et al*., 2002a
Hamamelis vernali	Vernal witch hazel	Styracaceae	Detached leaf dip in zoospore suspension	No	Leaf	Foliar necrosis	Hs	Parke *et al*., 2002a
Hamamelis virginiana	Virginian witch hazel	Hamamelidaceae	Mycelial plugs placed on detached wounded leaves	Yes	Leaf	Leaf and twig necrosis	Hs	Giltrap *et al*., 2004

Host name	Common name	Host family	Test method	Wounded?	Plant part tested	Symptom	Susceptibility*	Reference
Hebe imbricata	Hebe	Plantaginaceae	Mycelial discs on wounded petioles, stem bases or shoots	Yes	Petioles, stem bases, shoots	Details not supplied	Not given	Orlikowski & Szkuta, 2002
Heberdenia excelsa	Aderno, Sacatero	Lauraceae	Mycelial plug inoculum on leaf	Yes	Detached leaf	Leaf necrosis	Ls	Moralejo *et al*., *Personal Communication*
Hedera helix	Ivy	Araliaceae	Mycelial plug inoculum on leaf	Yes	Detached leaf	Leaf necrosis	Ls	Moralejo *et al*., *Personal Communication*
Hedera helix	Ivy	Araliaceae	Zoospore suspension dipping	No	Stem/Leaf	Lesion extension slight	Ls	Defra, PH0193S
Hedera helix	Ivy	Araliaceae	Mycelial plug inoculum on leaf	Yes	Leaf	Lesion extension slight	Ls	Defra, PH0193S
Hedera helix	Ivy	Araliaceae	Detached leaf dip in zoospore suspension	Details not supplied	Leaf	Details not supplied	R	Linderman *et al*., 2002
Heteromeles arbutifolia	Toyon	Rosaceae	Leaf inoculation by pinning a mycelial plug to the upper surface of leaves	Yes	Leaf	Leaf lesions	Ls	Garbelotto *et al*., 2003
Humulus lupulus	Golden hop	Cannabidaceae	Mycelial plug inoculum on leaf	Yes	Leaf	No necrosis or necrosis only in damaged tissue	Virtually immune	Defra, PH0193S
Hypericum 'Hidcote'	St. John's Wort	Hypericaceae	Detached leaf dip in zoospore suspension	No	Leaf	No symptoms were observed	Not given	Parke *et al*., 2002a
Ilex aquifolium	Holly	Aquifoliacea	Mycelial plug on twig	Yes	Twig cutting	Bark necrosis	Ms	Moralejo *et al*., *Personal Communication*
Ilex aquifolium	Holly	Aquifoliacea	Log inoculation	Yes	Inner bark	Inner bark necrosis	Ls - Ms	Moralejo *et al*., *Personal Communication*
Ilex aquifolium	Holly	Aquifoliaceae	Mycelial plug inoculum on leaf	Yes	Leaf	Lesion not extending much beyond wound	R	Defra, PH0193S
Ilex aquifolium	Holly	Fagaceae	Detached leaves dipped in zoospore suspensions	No	Leaf	Low proportion with leaf necrosis, low level of back isolation	R - Ls	Denman *et al*., 2005
Ilex aquifolium	Holly	Aquifoliaceae	Log inoculations	Yes	Inner bark	Inner bark death and bleeding cankers	Ls	Brasier *et al*., *Personal Communication*
Ilex aquifolium	Holly	Aquifoliaceae	Detached leaf dip in zoospore suspension	Details not supplied	Leaf	Details not supplied	R	Linderman *et al*., 2002
Ilex canariensis	Small leaved holly	Aquifoliaceae	Mycelial plug inoculum on leaf	Yes	Detached leaf	Leaf necrosis	Ms	Moralejo *et al*., *Personal Communication*
Ilex perado	Madeiran holly	Aquifoliaceae	Mycelial plug inoculum on leaf	Yes	Detached leaf	Leaf necrosis	Ls	Moralejo *et al*., *Personal Communication*
Ilex sp.	Holly	Aquifoliaceae	Leaf inoculation	Details not supplied	Leaf	Details not supplied	R	Inman *et al*., 2002
Kalmia angustifolia	Sheep laurel	Ericaceae	Mycelial discs on wounded petioles, stem bases or shoots	Yes	Petioles, stem bases, shoots	Leaf necrosis, stem blight	Not given	Orlikowski & Szkuta, 2002
Kalmia latifolia	Mountain laurel	Ericaceae	Details not supplied	Details not supplied	Details not supplied	Details not supplied	Not given	Orlikowski & Szkuta, 2002
Kalmia latifolia 'Madeline'	Mountain laurel	Ericaceae	Detached leaf dip in zoospore suspension	Details not supplied	Leaf	Details not supplied	Not given	Tooley & Englander, 2002
Laburnum anagyroides	Golden chain tree	Leguminosae	Detached leaf dip in zoospore suspension	No	Leaf	Foliar necrosis	Ls	Vannini, *Personal Communication*

Host name	Common name	Host family	Test method	Wounded?	Plant part tested	Symptom	Susceptibility*	Reference
Laburnum anagyroides	Golden chain tree	Leguminosae	Wounded stem tests using mycelial plugs	Yes	Stem	Bark necrosis	Hs	Vannini, *Personal Communication*
Lantana camara	Shrub verbena	Verbenaceae	Mycelial plug inoculum on leaf	Yes	Detached leaf	Leaf necrosis	Ms - Hs	Moralejo *et al*., *Personal Communication*
Larix occidentalis	Western larch	Pinaceae	Leaf dip in zoospore suspension	No	Leaf	Details not supplied	Ls - R	Hansen *et al*., 2005
Larix occidentalis	Western larch	Pinaceae	Stem susceptibility by wound inoculation with mycelial plugs	Yes	Stem	Details not supplied	Hs	Hansen *et al*., 2005
Larix occidentalis	Western larch	Pinaceae	Whole plant dip in zoospore suspension	No	Whole plant	Details not supplied	R	Hansen *et al*., 2005
Laurus nobilis	Bay laurel	Lauraceae	Wounded stem tests using mycelial plugs	Yes	Stem	Bark necrosis	Ls	Vannini, *Personal Communication*
Laurus nobilis	Bay laurel	Lauraceae	Detached leaf dip in zoospore suspension	No	Leaf	Foliar necrosis	Ls	Vannini, *Personal Communication*
Laurus nobilis	Bay laurel	Lauraceae	Mycelial plug inoculum on leaf	Yes	Leaf	No necrosis or necrosis only in damaged tissue	Virtually immune	Defra, PH0193S
Lavatera sp.	Tree mallow	Malvaceae	Mycelial plug inoculum on leaf	Yes	Leaf	No necrosis or necrosis only in damaged tissue	Virtually immune	Defra, PH0193S
Ledum palustre	Marsh tea, wild rosemary	Ericaceae	Details not supplied	Details not supplied	Leaves and stems	Leaf necrosis	Ls	Orlikowski & Szkuta, 2003
Ledum palustre	Marsh tea, wild rosemary	Ericaceae	Details not supplied	Details not supplied	Leaves and stems	Stem lesions	Ls	Orlikowski & Szkuta, 2003
Leucothoe fontanesiana	Girard's Rainbow dog hobble	Ericaceae	Mycelial plug inoculum on leaf	Yes	Leaf	Lesions very extensive	Hs	Defra, PH0193S
Leucothoe walteri	Drooping laurel	Ericaceae	Details not supplied	Details not supplied	Leaves	Leaf necrosis	Ls	Orlikowski & Szkuta, 2003
Leucothoe walteri	Drooping laurel	Ericaceae	Details not supplied	Details not supplied	Stems	Stem lesions	Ls	Orlikowski & Szkuta, 2003
Ligustrum sp.	Privet	Oleaceae	Mycelial plug inoculum on leaf	Yes	Leaf	Lesion not extending much beyond wound	R	Defra, PH0193S
Ligustrum vulgare	Common privet	Oleaceae	Mycelial plug inoculum on leaf	Yes	Detached leaf	Leaf necrosis	Ls	Moralejo *et al*., *Personal Communication*
Linnaea borealis	Twinflower	Caprifoliaceae	Detached leaf dip in zoospore suspension	Details not supplied	Leaf	Details not supplied	Ls	Zanzot *et al*., 2002
Liriodendron tulipifera	Tulip tree	Magnoliaceae	Log inoculations	Yes	Inner bark	Inner bark death and bleeding cankers	R	Brasier *et al*., *Personal Communication*
Lithocarpus densiflorus	Tanoak	Fagaceae	Leaf inoculation by pinning a mycelial plug to the upper surface of leaves	Yes	Leaf	Leaf lesions	Hs	Garbelotto *et al*., 2003
Lithocarpus densiflorus	Tanoak	Fagaceae	Leaf dip in zoospore suspension	No	Leaf	Details not supplied	Ls	Hansen *et al*., 2005
Lithocarpus densiflorus	Tanoak	Fagaceae	Stem susceptibility by wound inoculation with mycelial plugs	Yes	Stem	Girdled	Hs	Hansen *et al*., 2005
Lithocarpus densiflorus	Tanoak	Fagaceae	Whole plant dip in zoospore suspension	No	Whole plant	Dieback	Hs	Hansen *et al*., 2005

Host name	Common name	Host family	Test method	Wounded?	Plant part tested	Symptom	Susceptibility*	Reference
Lithocarpus densiflorus	Tanoak	Fagaceae	Log inoculations	Details not supplied	Inner bark	Large cankers	Hs	Hansen *et al*., 2005
Lithocarpus densiflorus	Tanoak	Fagaceae	Mycelial plugs	Yes	Tree trunk (mature tree)	Stem lesions bleeding	Hs	Rizzo *et al*., 2002
Lithocarpus densiflorus	Tanoak	Fagaceae	Mycelial plugs	Yes	Stems (seedlings)	Stem lesions some discolouration in xylem, wilting, stem girdling, lesion extension into petioles, seedling death	Hs	Rizzo *et al*., 2002
Lonicera implexa	Honeysuckle	Caprifoliaceae	Zoospore point inoculation	Yes	Detached leaf	Leaf necrosis	Ms	Moralejo *et al*., *Personal Communication*
Lonicera implexa	Honeysuckle	Caprifoliaceae	Detached leaf dip in zoospore suspension	No	Leaf	Necrotic lesions followed by extensive blight	Hs	Moralejo & Hernandez, 2002
Lonicera periclymenum	Common honeysuckle	Caprifoliaceae	Young plants inoculated through stem or leaf	Not specified	Stem/Leaf	No symptoms	Not given	de Gruyter *et al*., 2002
Lonicera periclymenum	Common honeysuckle	Caprifoliaceae	Mycelial plug inoculum on leaf	Yes	Leaf	Lesion extension slight	Ls	Defra, PH0193S
Lonicera periclymenum	Common honeysuckle	Caprifoliaceae	Stem susceptibility by wound inoculation with mycelial plugs	Yes	Stem	Lesion extension slight	Ls	Defra, PH0193S
Lonicera periclymenum	Common honeysuckle	Caprifoliaceae	Zoospore suspension dipping	No	Stem/Leaf	Lesion extension slight	Ls	Defra, PH0193S
Malus sp.	Apple	Rosaceae	Details not supplied	Details not supplied		Details not supplied	Ls	Inman *et al*., 2002
Malus sylvestris	Crab apple	Rosaceae	Mycelial plug inoculum on leaf	Yes	Leaf	Lesion extension slight	Ls	Defra, PH0193S
Morus sp.	Mulberry	Moraceae	Mycelial plug inoculum on leaf	Yes	Leaf	No necrosis or necrosis only in damaged tissue	Virtually immune	Defra, PH0193S
Myoporum pictum	Popwood, Sandalwood	Myoporaceae	Mycelial plug inoculum on leaf	Yes	Detached leaf	Leaf necrosis	Ls	Moralejo *et al*., *Personal Communication*
Myrica faya	Fire tree	Myricaceae	Mycelial plug inoculum on leaf	Yes	Detached leaf	Leaf necrosis	Ls - Ms	Moralejo *et al*., *Personal Communication*
Myrtus communis	Myrtle	Myrtaceae	Zoospore point inoculation	Yes	Detached leaf	Leaf necrosis	R - Ls	Moralejo *et al*., *Personal Communication*
Myrtus communis	Myrtle	Myrtaceae	Mycelial plug on twig	Yes	Twig cutting	Bark necrosis	R	Moralejo *et al*., *Personal Communication*
Nerium oleander	Oleander	Apocynaceae	Wounded stem tests using mycelial plugs	Yes	Stem	Bark necrosis	Ls	Vannini, *Personal Communication*
Nerium oleander	Oleander	Apocynaceae	Detached leaf dip in zoospore suspension	No	Leaf	Foliar necrosis	Ls	Vannini, *Personal Communication*
Nerium oleander	Oleander	Apocynaceae	Mycelial plug inoculum on leaf	Yes	Detached leaf	Details not supplied	R	Moralejo *et al*., *Personal Communication*
Nothofagus dombeyi	False beech	Fagaceae	Log inoculations	Yes	Inner bark	Inner bark death and bleeding cankers	Ms	Brasier *et al*., *Personal Communication*
Nothofagus obliqua	Roble beech	Fagaceae	Log inoculations	Yes	Inner bark	Inner bark death and bleeding cankers	Ms	Brasier *et al*., *Personal Communication*
Nothofagus procera	Rauli	Fagaceae	Log inoculations	Yes	Inner bark	Inner bark death and bleeding cankers	Ms	Brasier *et al*., *Personal Communication*

Host name	Common name	Host family	Test method	Wounded?	Plant part tested	Symptom	Susceptibility*	Reference
Ocothea foetens	Greenheart	Lauraceae	Mycelial plug inoculum on leaf	Yes	Detached leaf	Leaf necrosis	Ls	Moralejo *et al*., *Personal Communication*
Olea europaea	Olive	Oleaceae	Detached leaf dip in zoospore suspension	No	Leaf	Necrotic lesions followed by extensive blight	Hs	Moralejo & Hernandez, 2002
Olea europaea	Olive	Oleaceae	Mycelial plug on twig	Yes	Twig cutting	Bark necrosis	R	Moralejo *et al*., *Personal Communication*
Olea europaea	Olive	Oleaceae	Log inoculation	Yes	Inner bark	Inner bark necrosis	R	Moralejo *et al*., *Personal Communication*
Oxydendrum arboreum	Sourwood	Ericaceae	Detached leaf dip in zoospore suspension	No	Leaf	Foliar necrosis	Hs	Parke *et al*., 2002a
Pachysandra terminalis	Japanese pachysandra	Buxaceae	Detached leaf dip in zoospore suspension	Details not supplied	Leaf	Details not supplied	Not given	Linderman *et al*., 2002
Persea indica	Lauraceous tree	Lauraceae	Mycelial plug inoculum on leaf	Yes	Detached leaf	Leaf necrosis	Ls	Moralejo *et al*., *Personal Communication*
Philadelphus coronarius	Mock orange	Saxifragaceae	Detached leaf dip in zoospore suspension	No	Leaf	No symptoms were observed	Not given	Parke *et al*., 2002a
Photinia fraseri 'Red Robin'	Photinia	Rosaceae	Wounded stem tests using mycelial plugs	Yes	Stem	Bark necrosis	Ls - Ms	Vannini, *Personal Communication*
Photinia fraseri 'Red Robin'	Photinia	Rosaceae	Mycelial plugs	Details not supplied	Leaf base	Necrosis	Ms - Ls	Orlikowski & Szkuta, 2004
Photinia serrulata	Chinese photinia	Rosaceae	Detached leaf dip in zoospore suspension	No	Leaf	No symptoms were observed	Not given	Parke *et al*., 2002a
Photinia sp.	Christmas berry	Rosaceae	Mycelial plug inoculum on leaf	Yes	Leaf	Lesion well developed	Ms	Defra, PH0193S
Phyllirea latifolia	European holly	Oleaceae	Zoospore point inoculation	Yes	Detached leaf	Leaf necrosis	Ls	Moralejo *et al*., *Personal Communication*
Phyllirea latifolia	European holly	Oleaceae	Zoospore point inoculation	Yes	Detached leaf	Leaf necrosis	R	Moralejo *et al*., *Personal Communication*
Picconia excelsa	Southern olive	Oleaceae	Mycelial plug inoculum on leaf	Yes	Detached leaf	Leaf necrosis	Ls - Ms	Moralejo *et al*., *Personal Communication*
Picea abies	Norway spruce	Pinaceae	Log inoculations	Yes	Inner bark	Inner bark death and bleeding cankers	Ms	Brasier *et al*., *Personal Communication*
Picea abies	Norway spruce	Pinaceae	Detached leaves dipped in zoospore suspensions	No	Leaf	Details not supplied	Ls	Denman *et al*., 2005
Picea abies	Norway spruce	Pinaceae	Sapling stem inoculation	Yes	Stem	Stem lesion	Ls	Denman *et al*., *Personal Communication*
Picea sitchensis	Sitka spruce	Pinaceae	Sapling stem inoculation	Yes	Stem	Stem lesion	Ls	Denman *et al., Personal Communication*
Picea sitchensis	Sitka spruce	Pinaceae	Log inoculations	Yes	Inner bark	Inner bark death and bleeding cankers	Ms	Brasier *et al., Personal Communication*
Picea sitchensis	Sitka spruce	Pinaceae	Detached leaves dipped in zoospore suspensions	No	Leaf	Details not supplied	Ls	Denman *et al*., 2005
Picea sitchensis	Sitka spruce	Pinaceae	Leaf dip in zoospore suspension	No	Leaf	Details not supplied	Ls - Hs	Hansen *et al*., 2005
Picea sitchensis	Sitka spruce	Pinaceae	Stem susceptibility by wound inoculation with mycelial plugs	Yes	Stem	Details not supplied	Ls	Hansen *et al*., 2005

Host name	Common name	Host family	Test method	Wounded?	Plant part tested	Symptom	Susceptibility*	Reference
Picea sitchensis	Sitka spruce	Pinaceae	Whole plant dip in zoospore suspension	No	Whole plant	Details not supplied	R	Hansen *et al*., 2005
Picea sitchensis	Sitka spruce	Pinaceae	Log inoculations	Details not supplied	Inner bark	Details not supplied	Ms	Hansen *et al*., 2005
Pieris 'Brouwer's Beauty'	Mountain and Japanese pieris	Ericaceae	*In planta* foliage inoculations leaves still attached to potted plants either dipped into zoospore suspensions or inoculum sprayed onto leaves	No	Leaf, shoots and terminal buds	Leaf and stem necrosis, defoliation	Ms	Parke *et al*., 2004
Pieris floribunda	Fetterbush	Ericaceae	Detached leaf dip in zoospore suspension	Details not supplied	Leaf	Details not supplied	Not given	Tooley & Englander, 2002
Pieris formosa var. *forrestii*	Chinese pieris, Himalaya pieris	Ericaceae	Mycelial plugs inoculated onto wounded detached leaves	Yes	Leaf	Leaf lesions	Ms	Inman *et al*., 2003
Pieris japonica	Japanese pieris, Lily-of-the-valley bush	Ericaceae	Mycelial discs on wounded petioles, stem bases or shoots	Yes	Petioles (leaf), stem bases, shoots	Leaf necrosis, stem blight	Not given	Orlikowski & Szkuta, 2002
Pieris japonica	Japanese pieris, Lily-of-the-valley bush	Ericaceae	Mycelial plug inoculum on leaf	Yes	Leaf	Lesions very extensive	Hs	Defra, PH0193S
Pieris japonica 'Flaming Silver'	Japanese pieris, Lily-of-the-valley bush	Ericaceae	*In planta* foliage inoculations leaves still attached to potted plants either dipped into zoospore suspensions or inoculum sprayed onto leaves	No	Leaf, shoots and terminal buds	Leaf and stem necrosis, defoliation	Ms	Parke *et al*., 2004
Pieris japonica 'Prelude'	Pieris	Ericaceae	Mycelial plugs	Details not supplied	Leaf base	Necrosis	Ms	Orlikowski & Szkuta, 2004
Pieris japonica 'Variegata'	Variegated Japanese pieris	Ericaceae	*In planta* foliage inoculations leaves still attached to potted plants either dipped into zoospore suspensions or inoculum sprayed onto leaves	No	Leaf, shoots and terminal buds	Leaf and stem necrosis, defoliation	Ms	Parke *et al*., 2004
Pieris japonica x *formosa* 'Forest Flame'	Chinese pieris, Himalaya pieris	Ericaceae	*In planta* foliage inoculations leaves still attached to potted plants either dipped into zoospore suspensions or inoculum sprayed onto leaves	No	Leaf, shoots and terminal buds	Leaf and stem necrosis, defoliation	Ms	Parke *et al*., 2004
Pieris sp.	Pieris	Ericaceae	Details not supplied	Details not supplied		Details not supplied	Hs	Inman *et al*., 2002
Pinus contorta	Lodgepole pine	Pinaceae	Detached leaves dipped in zoospore suspensions	No	Leaf	Details not supplied	R	Denman *et al*., 2005
Pinus contorta	Lodgepole pine	Pinaceae	Sapling stem inoculation	Yes	Stem	Stem lesion	Hs	Denman *et al., Personal Communication*
Pinus contorta	Lodgepole pine	Pinaceae	Log inoculations	Yes	Inner bark	Inner bark death and bleeding cankers	R	Brasier *et al*., *Personal Communication*
Pinus contorta	Lodgepole pine	Pinaceae	Leaf dip in zoospore suspension	No	Leaf	Details not supplied	R	Hansen *et al*., 2005
Pinus contorta	Lodgepole pine	Pinaceae	Stem susceptibility by wound inoculation with mycelial plugs	Yes	Stem	Details not supplied	Ls	Hansen *et al*., 2005

Host name	Common name	Host family	Test method	Wounded?	Plant part tested	Symptom	Susceptibility*	Reference
Pinus contorta	Lodgepole pine	Pinaceae	Whole plant dip in zoospore suspension	No	Whole plant	Details not supplied	R	Hansen *et al*., 2005
Pinus contorta	Lodgepole pine	Pinaceae	Log inoculations	Details not supplied	Inner bark	Details not supplied	Ls	Hansen *et al*., 2005
Pinus halepensis	Aleppo pine	Pinaceae	Zoospore point inoculation	Yes	Detached leaf	Leaf necrosis	Ls	Moralejo *et al*., *Personal Communication*
Pinus halepensis	Aleppo pine	Pinaceae	Mycelial plug on twig	Yes	Twig cutting	Bark necrosis	Ls	Moralejo *et al*., *Personal Communication*
Pinus halepensis	Aleppo pine	Pinaceae	Log inoculation	Yes	Inner bark	Inner bark necrosis	Hs	Moralejo *et al*., *Personal Communication*
Pinus lambertiana	Sugar pine	Pinaceae	Whole plant dip in zoospore suspension	No	Whole plant	Details not supplied	R	Hansen *et al*., 2005
Pinus lambertiana	Sugar pine	Pinaceae	Leaf dip in zoospore suspension	No	Leaf	Details not supplied	Ls - R	Hansen *et al*., 2005
Pinus lambertiana	Sugar pine	Pinaceae	Stem susceptibility by wound inoculation with mycelial plugs	Yes	Stem	Details not supplied	Ls	Hansen *et al*., 2005
Pinus nigra	Black pine	Pinaceae	Log inoculation	Yes	Inner bark	Inner bark necrosis	Ls	Moralejo *et al*., *Personal Communication*
Pinus nigra var. *maritima*	Corsican pine	Pinaceae	Sapling stem inoculation	Yes	Stem	Stem lesion	Ls	Denman *et al*., *Personal Communication*
Pinus nigra var. *maritima*	Corsican pine	Pinaceae	Detached leaves dipped in zoospore suspensions	No	Leaf	Details not supplied	R	Denman *et al*., 2005
Pinus nigra var. *maritima*	Corsican pine	Pinaceae	Log inoculations	Yes	Inner bark	Inner bark death and bleeding cankers	R	Brasier *et al*., *Personal Communication*
Pinus pinaster	Maritime pine	Pinaceae	Log inoculation	Yes	Inner bark	Inner bark necrosis	Ls	Moralejo *et al*., *Personal Communication*
Pinus ponderosa	Ponderosa pine	Pinaceae	Leaf dip in zoospore suspension	No	Leaf	Details not supplied	R	Hansen *et al*., 2005
Pinus ponderosa	Ponderosa pine	Pinaceae	Stem susceptibility by wound inoculation with mycelial plugs	Yes	Stem	Details not supplied	R	Hansen *et al*., 2005
Pinus ponderosa	Ponderosa pine	Pinaceae	Whole plant dip in zoospore suspension	No	Whole plant	Details not supplied	R	Hansen *et al*., 2005
Pinus strobus	Western white pine	Pinaceae	Leaf dip in zoospore suspension	No	Leaf	Details not supplied	Ls	Hansen *et al*., 2005
Pinus strobus	Western white pine	Pinaceae	Whole plant dip in zoospore suspension	No	Whole plant	Details not supplied	R	Hansen *et al*., 2005
Pinus strobus	Western white pine	Pinaceae	Stem susceptibility by wound inoculation with mycelial plugs	Yes	Stem	Details not supplied	Hs	Hansen *et al*., 2005
Pinus sylvestris	Scots pine	Pinaceae	Log inoculation	Yes	Inner bark	Inner bark necrosis	Ls	Moralejo *et al*., *Personal Communication*
Pinus sylvestris	Scots pine	Pinaceae	Log inoculations	Yes	Inner bark	Inner bark death and bleeding cankers	R	Brasier *et al*., *Personal Communication*
Pinus sylvestris	Scots pine	Pinaceae	Detached leaves dipped in zoospore suspensions	No	Leaf	Details not supplied	R	Denman *et al*., 2005
Pinus sylvestris	Scots pine	Pinaceae	Sapling stem inoculation	Yes	Stem	Stem lesion	Ls	Denman *et al*., *Personal Communication*

Host name	Common name	Host family	Test method	Wounded?	Plant part tested	Symptom	Susceptibility*	Reference
Pistacia atlantica	Mastic tree	Anacardiaceae	Mycelial plug inoculum on leaf	Yes	Detached leaf	Leaf necrosis	Ls	Moralejo *et al*., *Personal Communication*
Pistacia lentiscus	Evergreen pistache mastic tree	Anacardiaceae	Detached leaf dip in zoospore suspension	No	Leaf	Necrotic lesions followed by extensive blight.	Hs	Moralejo & Hernandez, 2002
Pistacia lentiscus	Evergreen pistache mastic tree	Anacardiaceae	Zoospore point inoculation	Yes	Detached leaf	Leaf necrosis	Ms	Moralejo *et al*., *Personal Communication*
Pistacia lentiscus	Evergreen pistache mastic tree	Anacardiaceae	Mycelial plug on twig	Yes	Twig cutting	Bark necrosis	Ms	Moralejo *et al*., *Personal Communication*
Pistacia terebinthus	Turpentine tree	Anacardiaceae	Zoospore point inoculation	Yes	Detached leaf	Leaf necrosis	Ms	Moralejo *et al*., *Personal Communication*
Pittosporum tobira	Mock orange	Pittosporaceae	Mycelial plug inoculum on leaf	Yes	Detached leaf	Leaf necrosis	Ls	Moralejo *et al*., *Personal Communication*
Populus sp.	Hybrid poplar	Salicaceae	Stem susceptibility by wound inoculation with mycelial plugs	Yes	Stem	Details not supplied	R	Hansen *et al*., 2005
Populus tremula	Aspen	Salicaceae	Log inoculations	Yes	Inner bark	Inner bark death and bleeding cankers	R	Brasier *et al*., *Personal Communication*
Populus tremula	Aspen	Salicaceae	Detached leaves dipped in zoospore suspensions	No	Leaf	Medium proportion with leaf necrosis, low level of back isolation	R	Denman *et al*., 2005
Populus tremuloides	Quaking aspen	Salicaceae	Leaf dip in zoospore suspension	No	Leaf	Details not supplied	Ls	Hansen *et al*., 2005
Populus tremuloides	Quaking aspen	Salicaceae	Stem susceptibility by wound inoculation with mycelial plugs	Yes	Stem	Details not supplied	R	Hansen *et al*., 2005
Populus tremuloides	Quaking aspen	Salicaceae	Whole plant dip in zoospore suspension	No	Whole plant	Details not supplied	R	Hansen *et al*., 2005
Populus trichocarpa	Black cottonwood	Salicaceae	Stem susceptibility by wound inoculation with mycelial plugs	Yes	Stem	Details not supplied	R	Hansen *et al*., 2005
Populus trichocarpa	Black cottonwood	Salicaceae	Leaf dip in zoospore suspension	No	Leaf	Details not supplied	Ls	Hansen *et al*., 2005
Populus trichocarpa	Black cottonwood	Salicaceae	Whole plant dip in zoospore suspension	No	Whole plant	Details not supplied	R	Hansen *et al*., 2005
Prunus avium	Sweet cherry, wild cherry	Rosaceae	Detached leaves dipped in zoospore suspensions	No	Leaf	Low proportion with leaf necrosis, low level of back isolation	R - Ls	Denman *et al*., 2005
Prunus avium	Sweet cherry, wild cherry	Rosaceae	Log inoculations	Yes	Inner bark	Inner bark death and bleeding cankers	Ls	Brasier *et al*., *Personal Communication*
Prunus emarginata	Bitter cherry	Rosaceae	Whole plant dip in zoospore suspension	No	Whole plant	Details not supplied	Ls	Hansen *et al*., 2005
Prunus emarginata	Bitter cherry	Rosaceae	Stem susceptibility by wound inoculation with mycelial plugs	Yes	Stem	Details not supplied	Hs	Hansen *et al*., 2005
Prunus emarginata	Bitter cherry	Rosaceae	Leaf dip in zoospore suspension	No	Leaf	Details not supplied	Hs	Hansen *et al*., 2005
Prunus emarginata	Bitter cherry	Rosaceae	Log inoculations	Details not supplied	Inner bark	Details not supplied	Ls	Hansen *et al*., 2005
Prunus laurocerasus	Cherry laurel	Rosaceae	Log inoculations	Yes	Inner bark	Inner bark death and bleeding cankers	Ls	Brasier *et al*., *Personal Communication*
Prunus laurocerasus	Cherry laurel	Rosaceae	Zoospore suspension dipping	No	Stem/Leaf	Lesion extension slight	Ls	Defra, PH0193S

Host name	Common name	Host family	Test method	Wounded?	Plant part tested	Symptom	Susceptibility*	Reference
Prunus laurocerasus	Cherry laurel	Rosaceae	Mycelial plug inoculum on leaf	Yes	Leaf	Lesion extension slight	Ls	Defra, PH0193S
Prunus lusitanica	Portuguese laurel	Rosaceae	Zoospore suspension dipping	No	Stem/Leaf	Lesion extension slight	Ls	Defra, PH0193S
Prunus lusitanica	Portuguese laurel	Rosaceae	Mycelial plug inoculum on leaf	Yes	Leaf	Lesion extension slight	Ls	Defra, PH0193S
Prunus persica	Nectarine	Rosaceae	Mycelial plug inoculum on leaf	Yes	Leaf	Lesion extension slight	Ls	Defra, PH0193S
Prunus sp.	Ornamental cherry, stonefruits	Rosaceae	Mycelial plug inoculum on leaf	Yes	Leaf	Lesion extension slight	Ls	Defra, PH0193S
Pseudotsuga menziesii	Douglas fir	Pinaceae	Log inoculations	Yes	Inner bark	Inner bark death and bleeding cankers	Ms	Brasier *et al*., *Personal Communication*
Pseudotsuga menziesii	Douglas fir	Pinaceae	Detached leaves dipped in zoospore suspensions	No	Leaf	Details not supplied	Hs	Denman *et al*., 2005
Pseudotsuga menziesii	Douglas Fir	Pinaceae	Sapling stem inoculation	Yes	Stem	Stem lesion	Hs	Denman *et al*., *Personal Communication*
Pseudotsuga menziesii	Douglas fir	Pinaceae	Leaf dip in zoospore suspension	No	Leaf	Details not supplied	Ls	Hansen *et al*., 2005
Pseudotsuga menziesii	Douglas fir	Pinaceae	Mycelial plugs places in stem wounds	Yes	Stems	Dieback	Hs	Davidson *et al*., 2002
Pseudotsuga menziesii	Douglas fir	Pinaceae	Whole plant dip in zoospore suspension	No	Whole plant	Details not supplied	Ms	Hansen *et al*., 2005
Pseudotsuga menziesii	Douglas fir	Pinaceae	Log inoculations	Details not supplied	Inner bark	Details not supplied	Ms	Hansen *et al*., 2005
Pseudotsuga menziesii	Douglas fir	Pinaceae	Stem susceptibility by wound inoculation with mycelial plugs	Yes	Stem	Girdled	Ms	Hansen *et al*., 2005
Pseudotsuga menziesii	Douglas fir	Pinaceae	Mycelial plugs pinned onto misted leaves	Yes	Leaves/needles	Needle necrosis and shoot/sprout dieback	Hs	Davidson *et al*., 2002
Quercus agrifolia	Coast live oak	Fagaceae	Leaf inoculation by pinning a mycelial plug to the upper surface of leaves	Yes	Leaf	Leaf lesions	Ls	Garbelotto *et al*., 2003
Quercus agrifolia	Coast live oak	Fagaceae	Mycelial plugs	Yes	Tree trunk (mature trees)	Stem lesions bleeding	Hs	Rizzo *et al*., 2002
Quercus agrifolia	Coast live oak	Fagaceae	Mycelial plugs	Yes	Stems (saplings)	Stem lesions	Hs	Rizzo *et al*., 2002
Quercus agrifolia	Coast live oak	Fagaceae	Mycelial plugs	Yes	Stems (seedlings)	Stem lesions some discolouration in xylem	Hs	Rizzo *et al*., 2002
Quercus canariensis	African oak	Fagaceae	Log inoculation	Yes	Inner bark	Bark necrosis	Hs	Moralejo *et al*., *Personal Communication*
Quercus canariensis	African oak	Fagaceae	Mycelial plug on twig	Yes	Twig cutting	Bark necrosis	Ls	Moralejo *et al*. *Personal Communication*
Quercus cerris	Turkey oak	Fagaceae	Sapling stem inoculation	Yes	Stem	Stem lesion	Ls	Denman *et al*., *Personal Communication*
Quercus cerris	Turkey oak	Fagaceae	Details not supplied	Details not supplied	Inner bark	Details not supplied	Ms to two European isolates. Ls to North American isolates	Brasier *et al*., 2002

Host name	Common name	Host family	Test method	Wounded?	Plant part tested	Symptom	Susceptibility*	Reference
Quercus cerris	Turkey oak	Fagaceae	Log inoculations	Yes	Inner bark	Inner bark death and bleeding cankers	Ms to an European isolate	Brasier *et al*., *Personal Communication*
Quercus cerris	Turkey oak	Fagaceae	Detached leaves dipped in zoospore suspensions	No	Leaf	High proportion with leaf necrosis, high level of back isolation	Ms	Denman *et al*., 2005
Quercus chrysolepis	Canyon live oak	Fagaceae	Leaf dip in zoospore suspension	No	Leaf	Details not supplied	Ms	Hansen *et al*., 2005
Quercus chrysolepis	Canyon live oak	Fagaceae	Whole plant dip in zoospore suspension	No	Whole plant	Dieback	Ms	Hansen *et al*., 2005
Quercus chrysolepis	Canyon live oak	Fagaceae	Not specified (probably mycelial plugs)	Yes	Stems	Stem lesions	Ms	Murphy & Rizzo, 2003
Quercus chrysolepis	Canyon live oak	Fagaceae	Log inoculations	Details not supplied	Inner bark	Details not supplied	Ms	Hansen *et al*., 2005
Quercus chrysolepis	Canyon live oak	Fagaceae	Log inoculations	Details not supplied	Inner bark	Small lesions	Not given	Hansen *et al*., 2005
Quercus chrysolepis	Canyon live oak	Fagaceae	Stem susceptibility by wound inoculation with mycelial plugs	Yes	Stem	Details not supplied	Ms	Hansen *et al*., 2005
Quercus coccinea	Scarlet oak	Fagaceae	Log inoculations	Yes	Inner bark	Inner bark death and bleeding cankers	Ms	Brasier *et al*., *Personal Communication*
Quercus dentata	Japanese Emperor oak	Fagaceae	Wounded stem tests using mycelial plugs	Yes	Stem	Bark necrosis	Ls	Vannini, *Personal Communication*
Quercus douglasii	Blue oak	Fagaceae	Agar plug	Yes	Stem	Bark lesions	R	Rizzo *et al*., 2001
Quercus faginea	Portuguese oak	Fagaceae	Mycelial plug on twig	Yes	Twig cutting	Bark necrosis	Ls	Moralejo *et al*., *Personal Communication*
Quercus faginea	Portuguese oak	Fagaceae	Log inoculation	Yes	Inner bark	Bark necrosis	Ms	Moralejo *et al*., *Personal Communication*
Quercus falcata	Southern red oak	Fagaceae	Log inoculations	Yes	Inner bark	Inner bark death and bleeding cankers	Hs	Brasier *et al*., *Personal Communication*
Quercus garryana	Oregon white oak, Garry oak	Fagaceae	Stem susceptibility by wound inoculation with mycelial plugs	Yes	Stem	Details not supplied	Ls	Hansen *et al*., 2005
Quercus garryana	Oregon white oak, Garry oak	Fagaceae	Whole plant dip in zoospore suspension	Details not supplied	Whole plant	Details not supplied	R	Hansen *et al*., 2005
Quercus garryana	Oregon white oak, Garry oak	Fagaceae	Leaf dip in zoospore suspension	No	Leaf	Details not supplied	Ms	Hansen *et al*., 2005
Quercus garryana	Oregon white oak, Garry oak	Fagaceae	Log inoculations	Details not supplied	Inner bark	Details not supplied	Ms	Hansen *et al*., 2005
Quercus garryana	Oregon white oak, Garry oak	Fagaceae	Log inoculations	Details not supplied	Inner bark	Small lesions	Not given	Hansen *et al*., 2005
Quercus humilis	Downy oak	Fagaceae	Zoospore point inoculation	Yes	Detached leaf	Leaf necrosis	Ls	Moralejo *et al*., *Personal Communication*
Quercus ilex	Holm oak, Holly oak	Fagaceae	Detached leaf dip in zoospore suspension	No	Leaf	Foliar necrosis	Ls	Vannini, *Personal Communication*
Quercus ilex	Holm oak, Holly oak	Fagaceae	Mycelial plug on twig	Yes	Twig cutting	Bark necrosis	Ls	Moralejo *et al*., *Personal Communication*

Host name	Common name	Host family	Test method	Wounded?	Plant part tested	Symptom	Susceptibility*	Reference
Quercus ilex	Holm oak, Holly oak	Fagaceae	Detached leaf dip in zoospore suspension	No	Leaf	Limited lesion development	Ls	Moralejo & Hernandez, 2002
Quercus ilex	Holm oak, Holly oak	Fagaceae	Log inoculations	Yes	Inner bark	Inner bark necrosis	Ms	Moralejo *et al*., *Personal Communication*
Quercus ilex	Holm oak, Holly oak	Fagaceae	Zoospore point inoculation	Yes	Detached leaf	Leaf necrosis	Ls - Ms	Moralejo *et al*., *Personal Communication*
Quercus ilex	Holm oak, Holly oak	Fagaceae	Log inoculations	Yes	Inner bark	Inner bark death and bleeding cankers	Ms	Brasier *et al*., *Personal Communication*
Quercus ilex	Holm oak, Holly oak	Fagaceae	Details not supplied	Details not supplied	Details not supplied	Details not supplied	Ms	Brasier *et al*., 2002
Quercus ilex	Holm oak, Holly oak	Fagaceae	Detached leaves dipped in zoospore suspensions	No	Leaf	High proportion with leaf necrosis, high level of back isolation	Hs	Denman *et al*., 2005
Quercus kelloggii	Californian black oak	Fagaceae	Whole plant dip in zoospore suspension	Details not supplied	Whole plant	Dieback	Ms	Hansen *et al*., 2005
Quercus kelloggii	Californian black oak	Fagaceae	Leaf inoculation by pinning a mycelial plug to the upper surface of leaves	Yes	Leaf	Leaf lesions	Ls	Garbelotto *et al*., 2003
Quercus kelloggii	Californian black oak	Fagaceae	Log inoculations	Details not supplied	Inner bark	Details not supplied	Ls	Hansen *et al*., 2005
Quercus kelloggii	Californian black oak	Fagaceae	Leaf dip in zoospore suspension	No	Leaf	Details not supplied	Hs	Hansen *et al*., 2005
Quercus kelloggii	Californian black oak	Fagaceae	Log inoculations	Details not supplied	Inner bark	Small lesions	Not given	Hansen *et al*., 2005
Quercus kelloggii	Californian black oak	Fagaceae	Stem susceptibility by wound inoculation with mycelial plugs	Yes	Stem	Details not supplied	Ms	Hansen *et al*., 2005
Quercus lobata	Valley oak, California white oak	Fagaceae	Agar plug	Yes	Stem	None	R	Rizzo *et al*., 2001
Quercus macrolepis	Valonia oak	Fagaceae	Wounded stem tests using mycelial plugs	Yes	Stem	Bark necrosis	Ls	Vannini, *Personal Communication*
Quercus macrolepis	Valonia oak	Fagaceae	Detached leaf dip in zoospore suspension	No	Leaf	Foliar necrosis	Ls	Vannini, *Personal Communication*
Quercus palustris	Northern pin oak	Fagaceae	Log inoculations	Yes	Inner bark	Inner bark death and bleeding cankers	Ls	Brasier *et al*., *Personal Communication*
Quercus palustris	Northern pin oak	Fagaceae	Agar plug	Yes	Stem	Cambial and bark lesions	Hs	Rizzo *et al*., 2001
Quercus palustris	Northern pin oak	Fagaceae	Log inoculations	Details not supplied	Inner bark	Details not supplied	Ls - R	Hansen *et al*., 2005
Quercus petraea	Sessile oak, Durmast oak	Fagaceae	Detached leaves dipped in zoospore suspensions	No	Leaf	High proportion with leaf necrosis, high level of back isolation	Ms	Denman *et al*., 2005
Quercus petraea	Sessile oak, Durmast oak	Fagaceae	Log inoculations	Yes	Inner bark	Inner bark death and bleeding cankers	Ls	Brasier *et al*., *Personal Communication*
Quercus petraea	Sessile oak	Fagaceae	Sapling stem inoculation	Yes	Stem	Stem lesion	Ls	Denman *et al*., *Personal Communication*

Host name	Common name	Host family	Test method	Wounded?	Plant part tested	Symptom	Susceptibility*	Reference
Quercus pubescens	Downy oak	Fagaceae	Mycelial plug on twig	Yes	Twig cutting	Bark necrosis	Ls - Ms	Moralejo *et al*., *Personal Communication*
Quercus pubescens	Downy oak	Fagaceae	Log inoculation	Yes	Inner bark	Inner bark necrosis	Hs	Moralejo *et al*., *Personal Communication*
Quercus pyrenaica	Pyrenean oak	Fagaceae	Mycelial plug on twig	Yes	Twig cutting	Bark necrosis	Ls - Ms	Moralejo *et al*., *Personal Communication*
Quercus pyrenaica	Pyrenean oak	Fagaceae	Log inoculation	Yes	Inner bark	Inner bark necrosis	Hs	Moralejo *et al*., *Personal Communication*
Quercus pyrenaica	Pyrenean oak	Fagaceae	Zoospore point inoculation	Yes	Detached leaf	Leaf necrosis	Ls - Ms	Moralejo *et al*., *Personal Communication*
Quercus robur	English oak, Pedunculate oak, Common oak	Fagaceae	Spraying sporangia	Unspecified	Bark	All plants produced bark necrosis with occasional bleeding but necrosis on leaves was rare	Ms	Delatour *et al*., 2002
Quercus robur	English oak, Pedunculate oak, Common oak	Fagaceae	Wounded bark inoculations	Yes	Bark	All plants produced bark necrosis with occasional bleeding but necrosis on leaves was rare	Ms	Delatour *et al*., 2002
Quercus robur	English oak, Pedunculate oak, Common oak	Fagaceae	Mycelial plug on wounded stem	Yes	Stem	No symptoms	R	de Gruyter *et al*., 2002
Quercus robur	English oak, Pedunculate oak, Common oak	Fagaceae	Sapling stem inoculation	Yes	Stem	Stem lesion	Ls	Denman *et al*., *Personal Communication*
Quercus robur	English oak, Pedunculate oak, Common oak	Fagaceae	Detached leaves dipped in zoospore suspensions	No	Leaf	Low proportion with leaf necrosis, low level of back isolation	Ls	Denman *et al*., 2005
Quercus robur	English oak, Pedunculate oak, Common oak	Fagaceae	Log inoculations	Yes	Inner bark	Inner bark death and bleeding cankers	Ls	Brasier *et al*., *Personal Communication*
Quercus robur	English oak, Pedunculate oak, Common oak	Fagaceae	Mycelial plug inoculum on leaf	Yes	Leaf	Lesion not extending much beyond wound	R	Defra, PH0193S
Quercus rubra	Red oak	Fagaceae	Mycelial plug on wounded stem	Yes	Stem	Severe twig dieback	Ms	de Gruyter *et al*., 2002
Quercus rubra	Red oak	Fagaceae	Details not supplied	Details not supplied	Stems	Stem lesions	Ms	Orlikowski & Szkuta, 2003
Quercus rubra	Red oak	Fagaceae	Detached leaves dipped in zoospore suspensions	No	Leaf	Low proportion with leaf necrosis, low level of back isolation	R	Denman *et al*., 2005
Quercus rubra	Red oak	Fagaceae	Log inoculations	Yes	Inner bark	Inner bark death and bleeding cankers	Ms	Brasier *et al*., *Personal Communication*
Quercus rubra	Red oak	Fagaceae	Sapling stem inoculation	Yes	Stem	Stem lesion	Hs	Denman *et al*., *Personal Communication*
Quercus rubra	Red oak	Fagaceae	Stem susceptibility by wound inoculation with mycelial plugs	Yes	Stem	Details not supplied	Ms	Hansen *et al*., 2005

Host name	Common name	Host family	Test method	Wounded?	Plant part tested	Symptom	Susceptibility*	Reference
Quercus rubra	Red oak	Fagaceae	Agar plug	Yes	Stem	Cambial and bark lesions	Hs	Rizzo *et al*., 2001
Quercus suber	Cork oak	Fagaceae	Detached leaf dip in zoospore suspension	No	Leaf	Foliar necrosis	Ls	Vannini, *Personal Communication*
Quercus suber	Cork oak	Fagaceae	Log inoculation	Yes	Inner bark	Bark necrosis and bleeding	Ls	Moralejo *et al*., *Personal Communication*
Quercus suber	Cork oak	Fagaceae	Log inoculations	Yes	Inner bark	Inner bark death and bleeding cankers	Ls	Brasier *et al*., *Personal Communication*
Quercus suber	Cork oak	Fagaceae	Detached leaves dipped in zoospore suspensions	No	Leaf	Low proportion with leaf necrosis, low level of back isolation	R	Denman *et al*., 2005
Quercus trojana	Macedonian oak	Fagaceae	Detached leaf dip in zoospore suspension	No	Leaf	Foliar necrosis	Ls	Vannini, *Personal Communication*
Quercus trojana	Macedonian oak	Fagaceae	Wounded stem tests using mycelial plugs	Yes	Stem	Bark necrosis	Ls	Vannini, *Personal Communication*
Rhamnus alaternus	Italian buckthorn evergreen	Rhamnaceae	Zoospore point inoculation	Yes	Detached leaf	Leaf necrosis	Hs	Moralejo *et al*., *Personal Communication*
Rhamnus alaternus	Italian buckthorn evergreen	Rhamnaceae	Mycelial plug on twig	Yes	Twig cutting	Bark necrosis	Ls - Ms	Moralejo *et al*., *Personal Communication*
Rhamnus alaternus	Italian buckthorn evergreen	Rhamnaceae	Detached leaf dip in zoospore suspension	No	Leaf	Conspicuous necrotic lesions followed by extensive blight	Hs	Moralejo & Hernandez, 2002
Rhamnus californica	Coffeeberry	Cascara	Leaf inoculation by pinning a mycelial plug to the upper surface of leaves	Yes	Leaf	Leaf lesions	Ls	Garbelotto *et al*., 2003
Rhamnus purshiana	Cascara buckthorn	Rhamnaceae	Log inoculations	Details not supplied	Inner bark	Details not supplied	R	Hansen *et al*., 2005
Rhamnus purshiana	Cascara buckthorn	Rhamnaceae	Stem susceptibility by wound inoculation with mycelial plugs	Yes	Stem	Details not supplied	Ls	Hansen *et al*., 2005
Rhamnus purshiana	Cascara buckthorn	Rhamnaceae	Leaf dip in zoospore suspension	No	Leaf	Details not supplied	Ms	Hansen *et al*., 2005
Rhamnus purshiana	Cascara buckthorn	Rhamnaceae	Whole plant dip in zoospore suspension	No	Whole plant	Details not supplied	R	Hansen *et al*., 2005
Rhamnus purshiana	Cascara buckthorn	Rhamnaceae	Leaf dip in zoospore suspension	No	Leaf	Necrotic spots	Ms	Vettraino *et al*., 2006
Rhaphiolepis umbellata	Round-leaf hawthorn	Rosaceae	Detached leaf dip in zoospore suspension	No	Leaf	No symptoms were observed	R	Parke *et al*., 2002a
Rhododendron	Rhododendron	Ericaceae	Detached leaf dip in zoospore suspension	No	Leaf	Foliar necrosis	Ms	Vannini, *Personal Communication*
Rhododendron	Rhododendron	Ericaceae	Wounded stem tests using mycelial plugs	Yes	Stem	Bark necrosis	Ls	Vannini, *Personal Communication*
Rhododendron	Rhododendron	Ericaceae	Mycelial discs on wounded petioles, stem bases or shoots	Yes	Petioles (leaf), stem bases, shoots	Leaf necrosis, stem blight	Not given	Orlikowski & Szkuta, 2002
Rhododendron	Rhododendron	Ericaceae	Sapling stem inoculation	Yes	Stem	Stem lesion	Hs	Denman *et al*., *Personal Communication*
Rhododendron	Girard's rose' azalea	Ericaceae	Detached leaf dip in zoospore suspension	Details not supplied	Leaf	Leaf lesion	Not given	Tooley & Englander, 2002

Host name	Common name	Host family	Test method	Wounded?	Plant part tested	Symptom	Susceptibility*	Reference
Rhododendron	Azalea 'Northern Hilites'	Ericaceae	Detached leaf dip in zoospore suspension	Details not supplied	Leaf	Details not supplied	Hs	Tjosvold *et al*., 2002d
Rhododendron	Florist's azalea 'Inga'	Ericaceae	Detached leaf dip in zoospore suspension	Details not supplied	Leaf	Details not supplied	Not given	Tooley & Englander, 2002
Rhododendron	Rhododendron 'Cunningham's white'	Ericaceae	Detached leaf dip in zoospore suspension	Details not supplied	Leaf	Leaf lesion	Not given	Tooley & Englander, 2002
Rhododendron	Rhododendron 'Cunningham's white'	Ericaceae	Detached leaf dip in zoospore suspension	Details not supplied	Leaf	Details not supplied	Hs	Tjosvold *et al*., 2002d
Rhododendron	Rhododendron 'Exbury' hybrids	Ericaceae	Detached leaf dip in zoospore suspension	No	Leaf	Foliar necrosis	Hs	Parke *et al*., 2002a
Rhododendron	Azaleas	Ericaceae	Detached leaf using a mycelial inoculum plug	Details not supplied	Leaf	Details not supplied	Ms	Tjosvold *et al*., 2002d
Rhododendron catawbiense	Rhododendron	Ericaceae	Not specified	Not specified	Stem cuttings	Lesions	Not given	De Merlier *et al*., 2003
Rhododendron catawbiense	Rhododendron	Ericaceae	Zoospore suspension dipping	No	Stem/Leaf	Lesions very extensive	Hs	Defra, PH0193S
Rhododendron catawbiense	Rhododendron	Ericaceae	Stem susceptibility by wound inoculation with mycelial plugs	Yes	Stem	Lesions very extensive	Hs	Defra, PH0193S
Rhododendron catawbiense	Rhododendron	Ericaceae	Detached leaves dipped in zoospore suspensions	No	Leaf	High proportion with leaf necrosis, high level of back isolation	Hs	Denman *et al*., 2005
Rhododendron catawbiense	Rhododendron	Ericaceae	Mycelial plug inoculum on leaf	Yes	Leaf	Lesions very extensive	Hs	Defra, PH0193S
Rhododendron catawbiense 'Cunninghams White'	Rhododendron	Ericaceae	Mycelial plugs placed on abaxial surface of detached leaves	Yes	Leaves	Leaf necrosis	Not given	Žerjav *et al*., 2004
Rhododendron catawbiense 'Cunningham's White'	Rhododendron	Ericaceae	Details not supplied	Details not supplied	Leaves	Leaf lesions	Ms	Orlikowski & Szkuta, 2003
Rhododendron catawbiense 'Grandiflorum'	Rhododendron	Ericaceae	Wounded shoot tip using colonised mycelial plugs	Yes	Shoot tip	Twig blight, shoot tip dieback, brown spots on leaves	Hs	Werres *et al*., 2001
Rhododendron catawbiense 'Grandiflorum'	Rhododendron	Ericaceae	Colonised agar plugs added to water	Yes	Base of stem cutting	Twig blight, shoot tip dieback, brown spots on leaves	Hs	Werres *et al*., 2001
Rhododendron catawbiense 'Grandiflorum'	Rhododendron	Ericaceae	Base of stem end exposed to mycelial discs floating on water	Yes	Base of stem	Stem necrosis	Not rated	Lane *et al*., 2003
Rhododendron catawbiense 'H. Charmant'	Rhododendron	Ericaceae	Details not supplied	Details not supplied	Leaves	Leaf lesions	Ls	Orlikowski & Szkuta, 2003
Rhododendron catawbiense 'Haaga'	Rhododendron	Ericaceae	Details not supplied	Details not supplied	Leaves	Leaf lesions	Ms	Orlikowski & Szkuta, 2003
Rhododendron catawbiense 'Helliki'	Rhododendron	Ericaceae	Details not supplied	Details not supplied	Leaves	Leaf lesions	Ms	Orlikowski & Szkuta, 2003
Rhododendron catawbiense 'Lumina Jakushim'	Rhododendron	Ericaceae	Details not supplied	Details not supplied	Leaves	Leaf lesions	Ls	Orlikowski & Szkuta, 2003
Rhododendron catawbiense 'Mikkeli'	Rhododendron	Ericaceae	Details not supplied	Details not supplied	Leaves	Leaf lesions	Ms	Orlikowski & Szkuta, 2003
Rhododendron catawbiense 'Nova Zembla'	Rhododendron	Ericaceae	Mycelial plugs	Details not supplied	Leaf base	Necrosis	Ms - Hs	Orlikowski & Szkuta, 2004

Host name	Common name	Host family	Test method	Wounded?	Plant part tested	Symptom	Susceptibility*	Reference
Rhododendron catawbiense 'Nova Zembla'	Rhododendron	Ericaceae	Details not supplied	Details not supplied	Leaves	Leaf lesions	Ms	Orlikowski & Szkuta, 2003
Rhododendron catawbiense 'Pohjola's Daughter'	Rhododendron	Ericaceae	Details not supplied	Details not supplied	Leaves	Leaf lesions	Ms	Orlikowski & Szkuta, 2003
Rhododendron catawbiense 'Purple Splendour'	Rhododendron	Ericaceae	Details not supplied	Details not supplied	Leaves	Leaf lesions	Ms	Orlikowski & Szkuta, 2003
Rhododendron catawbiense 'Tiger stedli'	Rhododendron	Ericaceae	Details not supplied	Details not supplied	Leaves	Leaf lesions	Ms	Orlikowski & Szkuta, 2003
Rhododendron 'Cosmopolitan'	Rhododendron	Ericaceae	Detached leaves, either prick wounded or not, dipped in zoospore suspensions, or inoculated with a mycelial plug	Not specified	Leaves, tip or petiole	Leaf lesion	Not given	Heungens *et al*., 2003
Rhododendron 'Germania'	Rhododendron	Ericaceae	*In planta* inoculations (attached) leaves sprayed with zoospore suspension	Not specified	Leaves, tip or petiole	Leaf lesion	Ms	Heungens *et al*., 2003
Rhododendron 'Gomer Waterer'	Rhododendron	Ericaceae	Detached leaves, either prick wounded or not, dipped in zoospore suspensions, or inoculated with a mycelial plug	Not specified	Leaves, tip or petiole	Leaf lesion	Ms	Heungens *et al*., 2003
Rhododendron japonica	Azalea	Ericaceae	Mycelial plug inoculum on leaf	Yes	Leaf	Lesion not extending much beyond wound	R	Defra, PH0193S
Rhododendron japonica	Azalea	Ericaceae	Details not supplied	Details not supplied	Leaves and stems	Stem lesions	Ms	Orlikowski & Szkuta, 2003
Rhododendron 'Lachsgold'	Rhododendron	Ericaceae	Infested soil	Details not supplied	Details not supplied	Shoot necrosis plant death	Not given	Orlikowski & Szkuta, 2002
Rhododendron macrophyllum	Pacific rhododendron	Ericaceae	Whole plant dip in zoospore suspension	No	Whole plant	Dieback	Hs	Hansen *et al*., 2005
Rhododendron macrophyllum	Pacific rhododendron	Ericaceae	Leaf dip in zoospore suspension	No	Leaf	Details not supplied	Ms	Hansen *et al*., 2005
Rhododendron 'Marcel Menard'	Rhododendron	Ericaceae	Detached leaves, either prick wounded or not, dipped in zoospore suspensions, or inoculated with a mycelial plug	Not specified	Leaves, tip or petiole	Leaf lesion	Ms	Heungens *et al*., 2003
Rhododendron maximum	Rhododendron	Ericaceae	Detached leaf dip in zoospore suspension	No	Leaf	Leaf lesion	Not given	Tooley & Englander, 2002
Rhododendron 'Nova Zembla'	Rhododendron	Ericaceae	*In planta* foliage inoculations leaves still attached to potted plants either dipped into zoospore suspensions or inoculum sprayed onto leaves	No	Leaf, shoots and terminal buds	Foliage with necrosis, bud and stem death, necrotic lesions, leaf abscission	Hs	Parke *et al*., 2004
Rhododendron occidentale	Western azalea	Ericaceae	Detached leaf dip in zoospore suspension	No	Leaf	Details not supplied	Hs	Tjosvold *et al*., 2002d
Rhododendron ponticum	Rhododendron	Ericaceae	Seedlings inoculated with either EU or NA isolates	Not specified	Stem/Leaf	Severe stem/leaf lesions	Hs	de Gruyter *et al*., 2002
Rhododendron ponticum	Wild species	Ericaceae	Zoospore suspension dipping	No	Stem/Leaf	Lesions very extensive	Hs	Defra, PH0193S

Host name	Common name	Host family	Test method	Wounded?	Plant part tested	Symptom	Susceptibility*	Reference
Rhododendron ponticum	Rhododendron	Ericaceae	Log inoculations	Yes	Inner bark	Inner bark death and bleeding cankers	Ms	Brasier *et al*., *Personal Communication*
Rhododendron ponticum	Wild species	Ericaceae	Mycelial plug inoculum on leaf	Yes	Leaf	Lesions very extensive	Hs	Defra, PH0193S
Rhododendron ponticum	Wild species	Ericaceae	Stem susceptibility by wound inoculation with mycelial plugs	Yes	Stem	Lesions very extensive	Hs	Defra, PH0193S
Rhododendron ponticum 'Variegatum'	Rhododendron	Ericaceae	Detached leaves, either prick wounded or not, dipped in zoospore suspensions, or inoculated with a mycelial plug	Not specified	Leaves, tip or petiole	Leaf lesion	Ms	Heungens *et al*., 2003
Rhododendron simsii	Sim's azalea	Ericaceae	Dipped in zoospore suspension	Yes and No	Leaves	Leaf necrosis	Ls - R	Wagner *et al*., 2005
Rhododendron simsii	Sim's azalea	Ericaceae	Mycelial plug inoculum on leaf	Yes	Leaf	Lesion not extending much beyond wound	R	Defra, PH0193S
Rhododendron sp.	Azalea (I)	Ericaceae	Mycelial plug inoculum on leaf	Yes	Leaf	Lesion extension slight	Ls	Defra, PH0193S
Rhododendron sp.	Azalea (II)	Ericaceae	Mycelial plug inoculum on leaf	Yes	Leaf	No necrosis or necrosis only in damaged tissue	Virtually immune	Defra, PH0193S
Rhododendron yakushimanum 'Kalinka'	Rhododendron	Ericaceae	Detached leaves, either prick wounded or not, dipped in zoospore suspensions, or inoculated with a mycelial plug	Not specified	Leaves, tip or petiole	Leaf lesion	Ms	Heungens *et al*., 2003
Ribes sanguineum	Flowering currant, winter currant	Grossulariaceae	Detached leaf dip in zoospore suspension	No	Leaf	Foliar necrosis	Hs	Parke *et al*., 2002a
Robinia pseudacacia	Robinia	Leguminosae	Wounded stem tests using mycelial plugs	Yes	Stem	Bark necrosis	Ms	Vannini, *Personal Communication*
Robinia pseudacacia	Robinia	Leguminosae	Detached leaf dip in zoospore suspension	No	Leaf	Foliar necrosis	Ls	Vannini, *Personal Communication*
Rosa californica	California rose	Rosaceae	Detached foliage dipped into a zoospore suspension	Yes	Leaf	Leaf and petiole necrosis	Not rated, just given as susceptible	Hüberli *et al*., 2003
Rosa canina	Dog rose	Rosaceae	Zoospore suspension dipping	No	Stem/Leaf	Lesion extension slight	Ls	Defra, PH0193S
Rosa canina	Dog rose	Rosaceae	Mycelial plug inoculum on leaf	Yes	Leaf	Lesion extension slight	Ls	Defra, PH0193S
Rosa canina	Dog rose	Rosaceae	Stem susceptibility by wound inoculation with mycelial plugs	Yes	Stem	Lesion extension slight	Ls	Defra, PH0193S
Rosa gymnocarpa	Wood rose	Rosaceae	Detached foliage dipped into a zoospore suspension	Yes	Leaves	Leaf and petiole necrosis	Not rated, just given as susceptible	Hüberli *et al*., 2003
Rosa sempervirens	Evergreen rose	Rosaceae	Detached leaf dip in zoospore suspension	No	Leaf	Details not supplied	Ms	Moralejo & Hernandez, 2002
Rosa sempervirens	Evergreen rose	Rosaceae	Zoospore point inoculation	Yes	Detached leaf	Leaf necrosis	Ms	Moralejo *et al*., *Personal Communication*
Rosa sp.	Rose	Rosaceae	Mycelial plug inoculum on leaf	Yes	Detached leaf	Leaf necrosis	Hs	Moralejo *et al*., *Personal Communication*
Rubus fructicosus	Bramble	Rosaceae	Mycelial plug inoculum on leaf	Yes	Leaf	No necrosis or necrosis only in damaged tissue	Virtually immune	Defra, PH0193S

Host name	Common name	Host family	Test method	Wounded?	Plant part tested	Symptom	Susceptibility*	Reference
Rubus fructicosus	Bramble	Rosaceae	Zoospore suspension dipping	No	Stem/Leaf	No necrosis or necrosis only in damaged tissue	Virtually immune	Defra, PH0193S
Rubus specabilis	Salmonberry	Rosaceae	Whole plant dip in zoospore suspension	No	Whole plant	Details not supplied	Ls	Hansen *et al*., 2005
Rubus ulmifolius	Blackberry	Rosaceae	Zoospore point inoculation	Yes	Detached leaf	Leaf necrosis	R	Moralejo *et al*., *Personal Communication*
Rubus ulmifolius	Blackberry	Rosaceae	Detached leaf dip in zoospore suspension	No	Leaf	Details not supplied	R	Moralejo & Hernandez, 2002
Salix alba	White willow	Salicaceae	Detached leaf dip in zoospore suspension	No	Leaf	Foliar necrosis	Hs	Vannini, *Personal Communication*
Salix alba	White willow	Salicaceae	Wounded stem tests using mycelial plugs	Yes	Stem	Bark necrosis	Ls	Vannini, *Personal Communication*
Salix canariensis	Cascade willow	Salicaceae	Mycelial plug inoculum on leaf	Yes	Detached leaf	Leaf necrosis	Ls	Moralejo *et al*., *Personal Communication*
Salix caprea	Goat willow	Salicaceae	Detached leaf dip in zoospore suspension	No	Leaf	Foliar necrosis	Ls	Vannini, *Personal Communication*
Salix hookeriana	Hooker's willow	Salicaceae	Stem susceptibility by wound inoculation with mycelial plugs	Yes	Stem	Details not supplied	R	Hansen *et al*., 2005
Salix hookeriana	Hooker's willow	Salicaceae	Leaf dip in zoospore suspension	No	Leaf	Details not supplied	Ls - R	Hansen *et al*., 2005
Salix hookeriana	Hooker's willow	Salicaceae	Whole plant dip in zoospore suspension	No	Whole plant	Details not supplied	R	Hansen *et al*., 2005
Salix lasiandra	Pacific willow	Salicaceae	Leaf dip in zoospore suspension	No	Leaf	Details not supplied	R	Hansen *et al*., 2005
Salix lasiandra	Pacific willow	Salicaceae	Whole plant dip in zoospore suspension	No	Whole plant	Details not supplied	R	Hansen *et al*., 2005
Salix lasiandra	Pacific willow	Salicaceae	Stem susceptibility by wound inoculation with mycelial plugs	Yes	Stem	Details not supplied	R	Hansen *et al*., 2005
Salix sp.	Willow	Salicaceae	Log inoculations	Yes	Inner bark	Inner bark death and bleeding cankers	Ls	Brasier *et al*., *Personal Communication*
Sambucus nigra	Common elder	Caprifoliaceae	Stem susceptibility by wound inoculation with mycelial plugs	Yes	Stem	Lesions very extensive	Hs	Defra, PH0193S
Sambucus nigra	Common elder	Caprifoliaceae	Zoospore suspension dipping	No	Stem/Leaf	Lesions very extensive	Hs	Defra, PH0193S
Sambucus nigra	Common elder	Caprifoliaceae	Mycelial plug inoculum on leaf	Yes	Leaf	Lesions very extensive	Hs	Defra, PH0193S
Sambucus palmensis	Elderberry	Caprifoliaceae	Mycelial plug inoculum on leaf	Yes	Detached leaf	Leaf necrosis	Hs	Moralejo *et al*., *Personal Communication*
Sambucus racemosa	Red-berried elder	Caprifoliaceae	Mycelial plug inoculum on leaf	Yes	Leaf	Lesions very extensive	Hs	Defra, PH0193S
Sambucus sp.	Elderberry	Caprifoliaceae	Details not supplied	Details not supplied	Details not supplied	Details not supplied	Hs	Inman *et al*., 2002
Sequoia sempervirens	Coast redwood	Taxodiaceae	Detached leaves dipped in zoospore suspensions	No	Leaf	Details not supplied	Ms	Denman *et al*., 2005
Sequoia sempervirens	Coast redwood	Taxodiaceae	Log inoculations	Yes	Inner bark	Inner bark death and bleeding cankers	Ls	Brasier *et al*., *Personal Communication*
Sequoia sempervirens	Coast redwood	Taxodiaceae	Leaf dip in zoospore suspension	No	Leaf	Details not supplied	Ms - Hs	Hansen *et al*., 2005

Host name	Common name	Host family	Test method	Wounded?	Plant part tested	Symptom	Susceptibility*	Reference
Sequoia sempervirens	Coast redwood	Taxodiaceae	Whole plant dip in zoospore suspension	No	Whole plant	Details not supplied	Ms	Hansen *et al*., 2005
Sequoia sempervirens	Coast redwood	Taxodiaceae	Stem susceptibility by wound inoculation with mycelial plugs	Yes	Stem	Details not supplied	R	Hansen *et al*., 2005
Sequoia sempervirens	Coast redwood	Taxodiaceae	Mycelial plugs pinned onto misted leaves	Yes	Leaf/needles	Needle necrosis and shoot/sprout dieback	Ms	Maloney & Rizzo, 2002
Sequoia sempervirens	Coast redwood	Taxodiaceae	Mycelial plugs placed in stem wounds	Yes	Stems	Dieback	Ms	Maloney & Rizzo, 2002
Sequoia sempervirens	Coast redwood	Taxodiaceae	Log inoculations	Details not supplied	Inner bark	Details not supplied	Ls - R	Hansen *et al*., 2005
Sequoiadendron giganteum	Giant sequoia	Taxodiaceae	Stem susceptibility by wound inoculation with mycelial plugs	Yes	Stem	Details not supplied	R	Hansen *et al*., 2005
Skimmia japonica	Japanese skimmia	Rutaceae	Mycelial plug inoculum on leaf	Yes	Leaf	No necrosis or necrosis only in damaged tissue	Virtually immune	Defra, PH0193S
Smilax aspera	Greenbrier	Liliaceae	Detached leaf dip in zoospore suspension	No	Leaf	Details not supplied	Ls	Moralejo & Hernandez, 2002
Smilax aspera	Greenbrier	Liliaceae	Zoospore point inoculation	Yes	Detached leaf	Leaf necrosis	Ls	Moralejo *et al*., *Personal Communication*
Sorbus aucuparia	Mountain ash	Rosaceae	Wounded stem tests using mycelial plugs	Yes	Stem	Bark necrosis	Ls	Vannini, *Personal Communication*
Sorbus aucuparia	Mountain ash	Rosaceae	Detached leaf dip in zoospore suspension	No	Leaf	Foliar necrosis	Ls	Vannini, *Personal Communication*
Spiraea japonica	Japanese spirea	Rosaceae	Mycelial plug inoculum on leaf	Yes	Leaf	No necrosis or necrosis only in damaged tissue	Virtually immune	Defra, PH0193S
Symphoricarpus albus	Snowberry	Caprifoliaceae	Leaf inoculation	Yes	Leaf	Details not supplied	Ms	Inman *et al*., 2002
Symphoricarpus albus	Snowberry	Caprifoliaceae	Mycelial plug inoculum on leaf	Yes	Leaf	Lesion well developed	Ms	Defra, PH0193S
Syringa vulgaris	Common lilac	Oleaceae	Zoospore suspension dipping	No	Stem/Leaf	Lesions very extensive	Hs	Defra, PH0193S
Syringa vulgaris	Common lilac	Oleaceae	Mycelial plugs	No	Detached leaf	Leaf necrosis	Not rated, just given as susceptible	Beales *et al*., 2004b
Syringa vulgaris	Common lilac	Oleaceae	Stem susceptibility by wound inoculation with mycelial plugs	Yes	Stem	Lesions very extensive	Hs	Defra, PH0193S
Syringa vulgaris	Common lilac	Oleaceae	Mycelial plug inoculum on leaf	Yes	Leaf	Lesions very extensive	Hs	Defra, PH0193S
Tamus communis	Black bryony	Dioscoraceae	Zoospore point inoculation	Yes	Detached leaf	Leaf necrosis	R	Moralejo *et al*., *Personal Communication*
Taxus baccata	English yew	Taxodiaceae	Log inoculations	Yes	Inner bark	Inner bark death and bleeding cankers	Ls	Brasier *et al*., *Personal Communication*
Taxus baccata	English yew	Taxodiaceae	Mycelial plug inoculations	Yes	Needles on detached stem	Needle necrosis and stem die back	Not rated, just given as susceptible	Lane *et al*., 2004
Taxus baccata	English yew	Taxodiaceae	Sapling stem inoculation	Yes	Stem	Stem lesion	Ms	Denman *et al*., *Personal Communication*
Taxus baccata	English yew	Taxodiaceae	Detached leaves dipped in zoospore suspensions	No	Leaf	Needles showing necrosis	Ms - Ls	Denman *et al*., 2005

Host name	Common name	Host family	Test method	Wounded?	Plant part tested	Symptom	Susceptibility*	Reference
Taxus brevifolia	Pacific yew	Taxodiaceae	Leaf dip in zoospore suspension	No	Leaf	Details not supplied	Ls	Hansen *et al*., 2005
Taxus brevifolia	Pacific yew	Taxodiaceae	Whole plant dip in zoospore suspension	No	Whole plant	Details not supplied	Ms	Hansen *et al*., 2005
Taxus brevifolia	Pacific yew	Taxodiaceae	Stem susceptibility by wound inoculation with mycelial plugs	Yes	Stem	Details not supplied	Ms	Hansen *et al*., 2005
Thuja plicata	Western red cedar	Cupressaceae	Whole plant dip in zoospore suspension	No	Whole plant	Details not supplied	R	Hansen *et al*., 2005
Thuja plicata	Western red cedar	Cupressaceae	Stem susceptibility by wound inoculation with mycelial plugs	Yes	Stem	Details not supplied	Ls	Hansen *et al*., 2005
Thuja plicata	Western red cedar	Cupressaceae	Leaf dip in zoospore suspension	No	Leaf	Details not supplied	R	Hansen *et al*., 2005
Thuja plicata	Western red cedar	Cupressaceae	Log inoculations	Details not supplied	Inner bark	Details not supplied	Ls - R	Hansen *et al*., 2005
Tilia cordata	Small-leaved lime, Small-leaved linden	Tiliaceae	Log inoculations	Yes	Inner bark	Inner bark death and bleeding cankers	R	Brasier *et al*., *Personal Communication*
Tilia cordata	Small-leaved lime, Small-leaved linden	Tiliaceae	Mycelial plug inoculum on leaf	Yes	Leaf	Lesion well developed	Ms	Defra, PH0193S
Tilia cordata	Small-leaved lime, Small-leaved linden	Tiliaceae	Detached leaves dipped in zoospore suspensions	No	Leaf	Low proportion with leaf necrosis, high level of back isolation	Ls	Denman *et al*., 2005
Toxicodendron diversilobum	Poison oak	Taxodiaceae	Stem susceptibility by wound inoculation with mycelial plugs	Yes	Stem	Details not supplied	Ms	Hansen *et a*l., 2005
Toxicodendron diversilobum	Poison oak	Taxodiaceae	Leaf dip in zoospore suspension	No	Leaf	Details not supplied	Ms	Hansen *et al*., 2005
Trientalis latifolia	Starflower	Primulaceae	Leaves dipped in zoospore suspensions (leaves still attached to plants)	No	Leaf	Leaf necrosis	Hs	Hüberli *et al*., 2003
Tsuga heterophylla	Western hemlock	Pinaceae	Log inoculations	Yes	Inner bark	Inner bark death and bleeding cankers	Ls	Brasier *et al*., *Personal Communication*
Tsuga heterophylla	Western hemlock	Pinaceae	Detached leaves dipped in zoospore suspensions	No	Leaf	Details not supplied	Ms - Ls	Denman *et al*., 2005
Tsuga heterophylla	Western hemlock	Pinaceae	Sapling stem inoculation	Yes	Stem	Stem lesion	Hs	Denman *et al*., *Personal Communication*
Tsuga heterophylla	Western hemlock	Pinaceae	Stem susceptibility by wound inoculation with mycelial plugs	Yes	Stem	Details not supplied	Hs	Hansen *et al*., 2005
Tsuga heterophylla	Western hemlock	Pinaceae	Leaf dip in zoospore suspension	No	Leaf	Details not supplied	Ms	Hansen *et al*., 2005
Tsuga heterophylla	Western hemlock	Pinaceae	Whole plant dip in zoospore suspension	No	Whole plant	Details not supplied	R	Hansen *et al*., 2005
Tsuga heterophylla	Western hemlock	Pinaceae	Log inoculations	Details not supplied	Inner bark	Details not supplied	Ls	Hansen *et al*., 2005
Ulmus campestre	English elm	Ulmaceae	Detached leaf dip in zoospore suspension	No	Leaf	Foliar necrosis	Ms	Vannini, *Personal Communication*
Ulmus glabra	Wych elm	Ulmaceae	Stem susceptibility by wound inoculation with mycelial plugs	Yes	Stem	Lesion well developed	Ms	Defra, PH0193S
Ulmus glabra	Wych elm	Ulmaceae	Mycelial plug inoculum on leaf	Yes	Leaf	Lesion well developed	Ms	Defra, PH0193S
Ulmus glabra	Wych elm	Ulmaceae	Zoospore suspension dipping	No	Stem/Leaf	Lesion well developed	Ms	Defra, PH0193S

Host name	Common name	Host family	Test method	Wounded?	Plant part tested	Symptom	Susceptibility*	Reference
Ulmus minor	Small-leaved elm	Ulmaceae	Wounded stem tests using mycelial plugs	Yes	Stem	Bark necrosis	Ls - Ms	Vannini, *Personal Communication*
Ulmus minor	Small-leaved elm	Ulmaceae	Detached leaf dip in zoospore suspension	No	Leaf	Foliar necrosis	Ls	Vannini, *Personal Communication*
Ulmus minor	Small-leaved elm	Ulmaceae	Mycelial plug on twig	Yes	Twig cutting	Bark necrosis	Ls	Moralejo *et al*., *Personal Communication*
Ulmus minor	Small-leaved elm	Ulmaceae	Zoospore point inoculation	Yes	Detached leaf	Leaf necrosis	Ls	Moralejo *et al*., *Personal Communication*
Ulmus minor	Small-leaved elm	Ulmaceae	Mycelial plug inoculum on leaf	Yes	Detached leaf	Leaf necrosis	Ms - Hs	Moralejo *et al*., *Personal Communication*
Ulmus procera	English elm	Ulmaceae	Detached leaves dipped in zoospore suspensions	No	Leaf	High proportion with leaf necrosis, high level of back isolation	Hs - Ms	Denman *et al*., 2005
Ulmus procera	English elm	Ulmaceae	Log inoculations	Yes	Inner bark	Inner bark death and bleeding cankers	R	Brasier *et al*., *Personal Communication*
Ulmus sp.	Ornamental Scots elm	Ulmaceae	Mycelial plug inoculum on leaf	Yes	Leaf	Lesion well developed	Ms	Defra, PH0193S
Umbellularia californica	Californian bay laurel, Oregon myrtle	Lauraceae	Detached leaves dipped in zoospore suspensions	No	Leaf	High proportion with leaf necrosis, high level of back isolation	Hs - Ms	Denman *et al*., 2005
Umbellularia californica	Californian bay laurel, Oregon myrtle	Lauraceae	Mycelial plug inoculum on leaf	Yes	Leaf	Lesion extension slight	Ls	Defra, PH0193S
Umbellularia californica	Californian bay laurel, Oregon myrtle	Lauraceae	Zoospore suspension dipping	No	Stem/Leaf	Lesion extension slight	Ls	Defra, PH0193S
Umbellularia californica	Oregon myrtlewood	Lauraceae	Log inoculations	Details not supplied	Inner bark	Details not supplied	R	Hansen *et al*., 2005
Umbellularia californica	Oregon myrtlewood	Lauraceae	Leaf dip in zoospore suspension	No	Leaf	Details not supplied	Ls	Hansen *et al*., 2005
Umbellularia californica	Oregon myrtlewood	Lauraceae	Stem susceptibility by wound inoculation with mycelial plugs	Yes	Stem	Details not supplied	Ls	Hansen *et al*., 2005
Umbellularia californica	Oregon myrtlewood	Lauraceae	Leaf inoculation by pinning a mycelial plug to the upper surface of leaves	Yes	Leaf	Leaf lesions	Ls	Garbelotto *et al*., 2003
Umbellularia californica	Oregon myrtlewood	Lauraceae	Whole plant dip in zoospore suspension	No	Whole plant	Details not supplied	R	Hansen *et al*., 2005
Vaccinium membranaceum	Big huckleberry	Ericaceae	Leaf dip in zoospore suspension	No	Leaf	Details not supplied	Hs	Hansen *et al*., 2005
Vaccinium myrtillus	European wild blueberry	Ericaceae	Young plants inoculated through stem or leaf tissue	Not specified	Stem/Leaf	Plant death	Hs	de Gruyter *et al*., 2002
Vaccinium ovatum	Evergreen huckleberry	Ericaceae	Leaf inoculation by pinning a mycelial plug to the upper surface of leaves	Yes	Leaf	Leaf lesions	Ms	Garbelotto *et al*., 2003
Vaccinium ovatum	Evergreen huckleberry	Ericaceae	Whole plant dip in zoospore suspension	No	Whole plant	Details not supplied	Hs	Hansen *et al*., 2005
Vaccinium ovatum	Evergreen huckleberry	Ericaceae	Leaf dip in zoospore suspension	No	Leaf	Details not supplied	Hs	Hansen *et al*., 2005

Host name	Common name	Host family	Test method	Wounded?	Plant part tested	Symptom	Susceptibility*	Reference
Vaccinium parvifolium	Red huckleberry	Ericaceae	Detached leaf dip in zoospore suspension	Details not supplied	Details not supplied	Details not supplied	Not given	Zanzot *et al*., 2002
Vaccinium parvifolium	Red huckleberry	Ericaceae	Leaf dip in zoospore suspension	No	Leaf	Details not supplied	Hs	Hansen *et al*., 2005
Vaccinium sp.	Blueberry	Ericaceae	Mycelial plug inoculum on leaf	Yes	Leaf	Lesion not extending much beyond wound	R	Defra, PH0193S
Vaccinium vitis-idaea	Mountain cranberry	Ericaceae	Details not supplied	Details not supplied	Leaves and stems	Stem lesions	Ms	Orlikowski & Szkuta, 2003
Vaccinium vitis-idaea	Lingonberry	Ericaceae	Detached leaf dip in zoospore suspension	No	Leaf	Foliar necrosis and dieback	Not given	Parke *et al*., 2002b
Viburnum davidii	Viburnum	Caprifoliaceae	Stem susceptibility by wound inoculation with mycelial plugs	Yes	Stem	Lesion extension slight	Ls	Defra, PH0193S
Viburnum davidii	Viburnum	Caprifoliaceae	Mycelial plug inoculum on leaf	Yes	Leaf	Lesion extension slight	Ls	Defra, PH0193S
Viburnum davidii	Viburnum	Ericaceae	Detached leaf dip in zoospore suspension	Details not supplied	Leaf	Details not supplied	Not given	Linderman *et al*., 2002
Viburnum lucidum	Northern arrow wood	Caprifoliaceae	Mycelial plug inoculum on leaf	Yes	Detached leaf	Leaf necrosis	Hs	Moralejo *et al*., *Personal Communication*
Viburnum opulus	Guelder rose	Caprifoliaceae	Mycelial plug inoculum on leaf	Yes	Leaf	Lesion not extending much beyond wound	R	Defra, PH0193S
Viburnum plicatum var. *tomonentosum*	Viburnum	Ericaceae	Detached leaf dip in zoospore suspension	Details not supplied	Leaf	Details not supplied	Not given	Linderman *et al*., 2002
Viburnum plicatum var. *tormentosum* 'Mariesii'	Viburnum	Ericaceae	*In planta* foliage inoculations leaves still attached to potted plants either dipped into zoospore suspensions or inoculum sprayed onto leaves	No	Leaves, shoots, terminal buds	Leaf necrosis and defoliation	Ms	Parke *et al*., 2004
Viburnum tinus	Laurustinus	Caprifoliaceae	Spraying sporangia	No	Leaf	Foliar necrosis which could be limited or large	Not given	Delatour *et al*., 2002
Viburnum tinus	Viburnum	Caprifoliaceae	Detached leaf dip in zoospore suspension	No	Leaf	Foliar necrosis	Ls	Vannini, *Personal Communication*
Viburnum tinus	Laurustinus	Caprifoliaceae	Mycelial plug on twig	Yes	Twig cutting	Bark necrosis	Hs	Moralejo *et al*., *Personal Communication*
Viburnum tinus	Laurustinus	Caprifoliaceae	Zoospore point inoculation	Yes	Detached leaf	Leaf necrosis	Hs	Moralejo *et al*., *Personal Communication*
Viburnum tinus	Viburnum	Caprifoliaceae	Stem susceptibility by wound inoculation with mycelial plugs	Yes	Stem	Lesion well developed	Ms	Defra, PH0193S
Viburnum tinus	Viburnum	Caprifoliaceae	Mycelial plug inoculum on leaf	Yes	Leaf	Lesion well developed	Ms	Defra, PH0193S
Viburnum tinus	Viburnum	Caprifoliaceae	Detached leaf dip in zoospore suspension	No	Leaf	Foliar necrosis	Hs	Parke *et al*., 2002a
Viburnum tinus subsp. *rigidum*	Guelder Rose	Caprifoliaceae	Mycelial plug inoculum on leaf	Yes	Detached leaf	Leaf necrosis	Hs	Moralejo *et al*., *Personal Communication*
Viburnum x *bodnantense*	Viburnum	Ericaceae	Young plants inoculated through stem or leaf tissue	Not specified	Stem/leaf	Free of damage	R	de Gruyter *et al*., 2002
Visnea mocanera	Mocan	Lauraceae	Mycelial plug inoculum on leaf	Yes	Detached leaf	Leaf necrosis	R	Moralejo *et al*., *Personal Communication*

Host name	Common name	Host family	Test method	Wounded?	Plant part tested	Symptom	Susceptibility*	Reference
Vitis vinifera	Grapevine	Vitaceae	Mycelial plug inoculum on leaf	Yes	Leaf	No necrosis or necrosis only in damaged tissue	Virtually immune	Defra, PH0193S
Weigela sp.	Weigela	Caprifoliaceae	Mycelial plug inoculum on leaf	Yes	Leaf	No necrosis or necrosis only in damaged tissue	Virtually immune	Defra, PH0193S
Zenobia pulverulenta	Dusty zenobia	Ericaceae	Detached leaf dip in zoospore suspension	No	Leaf	Leaf lesion	Not given	Tooley & Englander, 2002

Appendix 3. Monitoring results for the presence of *Phytophthora ramorum* on the territory of the Member States in 2004-2006

Table 1. Monitoring results for the presence of *Phytophthora ramorum* on the territory of the Member States in 2004

Country	Nurseries + Garden Centres			Public Green Sites			Forestry Sites			Total outbreaks per country
	No of visual inspections	No of lab analysis of samples taken	No of outbreak sites	No of visual inspections	No of lab. analysis of samples taken	No of outbreak sites	No of visual inspections	No of lab analysis of samples taken	No of outbreak sites	
Austria	106	36	0	341	6	0	213	39	0	0
Belgium	651	543	45	47	21	2	4	2	0	47
Cyprus	53	0	0	0	0	0	0	0	0	0
Czech Rep.	265	13	0	146	6	0	40	1	0	0
Denmark	680	82	10	8	2	0	8	1	0	10
Estonia	38	48	0	1	1	0	0	0	0	0
Finland	241	247	13	17	24	0	0	0	0	13
France	1974	788	23	169	18	0	61	77	0	23
Germany	1560	56	6	591	49	0	107	146	2	8
Hungary	39	2	0	79*	1	0	24355**	0	0	0
Ireland	42	42	2	211	211	1	285	285	1	4
Italy	270	7	0	53	2	0	0	-	-	0
Latvia	31	16	0	12	11	0	3	0	0	0
Lithuania	29	40	0	14	8	0	8	4	0	0
Netherlands	1500	65	9	167	136	7	103	84	6	22
Malta	9	3	0	11	3	0	1	0	0	0
Poland	3975	84	0	1197	13	0	1113	3	0	0
Portugal	5	8	0	0	0	0	0	0	0	0
Slovakia	30	1	0	37	1	0	9	2	0	0
Slovenia	134	72	10	81	85	1	35	4	0	11
Spain	390	749	23	271	122	0	48	23	0	23
Sweden	105	23	2	19	1	0	0	0	0	2
UK	21216	2388	112	8063	5415	55	1575	377	0	167
TOTAL	33343	5313	255	11535	6136	66	3613	1048	9	330

*Number of inspections in both public green sites and forestry sites; **Number of plant inspected; No results for Greece and Luxembourg.

Table 2. Monitoring results for the presence of *Phytophthora ramorum* on the territory of the Member States in 2005

Country	Nurseries + Garden Centres			Public Green Sites			Forestry Sites			Total outbreaks per country
	No of visual inspections	No of lab analysis of samples taken	No of outbreak sites	No of visual inspections	No of lab. analysis of samples taken	No of outbreak sites	No of visual inspections	No of lab analysis of samples taken	No of outbreak sites	
Austria	158	31	0	16	9	0	4751	13	0	0
Belgium	467	242	13	116***	9***	0***	-	-	-	13
Cyprus	34	10	0	2	0	0	11	1	0	0
Czech Rep.	290	19	0	211	8	0	63	0	0	0
Denmark	610	97	15	40	19	1	12	0	0	16
Estonia	47	56	0	5	5	0	5	5	0	0
France	1789	567	14	151	7	0	40	25	0	14
Germany	1388	135	14	482	44	1	102	67	2	17
Hungary	195	15*	0	122	1	0	196	-	0	0
Ireland	322	322	20	109	109	1	228	228	2	23
Latvia	24	16	0	17	15	0	0	0	0	0
Lithuania	44	20	0	8	4	0	4	1	0	0
Netherlands	1600	7	2	128**	25**	7**	-	-	-	9
Malta	3	5	0	18	9	0	2	2	0	0
Poland	4298	250	0	955	25	0	899	4	0	0
Portugal	14	18	0	0	0	0	0	0	0	0
Slovakia	87	8	0	178	0	0	13	-	-	0
Slovenia	84	93	5	21	45	1	32	0	0	6
Spain	430	159	6	152	50	0	361	28	0	6
Sweden	133	14	2	39	6	0	-	-	-	2
UK	27151	1730	112	11757	7535	70	173	37	9	191
TOTAL	39168	3799	203	14527	7925	81	6892	426	13	297

*15 samples taken from all three sites; **Figures shown are for both public green sites and forestry sites; ***Figures shown are for both public green and forestry sites;
No results for Finland, Greece, Italy and Luxembourg.

Table 3. Monitoring results for the presence of *Phytophthora ramorum* on the territory of the Member States in 2006

Country	Nurseries + Garden Centres			Public Green Sites			Forestry Sites			Total outbreaks per country
	No of visual inspections	No of lab analysis of samples taken	No of outbreak sites	No of visual inspections	No of lab. analysis of samples taken	No of outbreak sites	No of visual inspections	No of lab analysis of samples taken	No of outbreak sites	
Austria	118	33	0	59	9	0	1192	0	0	0
Belgium	237	156	8	153	1	0	0	-	-	8
Cyprus	25	5	0	0	0	0	13	0	0	0
Czech Rep.	356	14	0	273	4	0	65	0	0	0
Denmark	600	26	3	29	21	1	6	10	0	4
Estonia	95	47	2	61	9	0	13	4	0	2
Finland	199	132	10	25	4	0	0	0	0	10
France	1693	377	18	59	16	0	33	16	0	18
Hungary	194	-	0	116	5	0	206	2	-	0
Ireland	95	280	13	21	59	2	21	367	3	18
Latvia	62	17	0	27	18	0	1	2	0	0
Lithuania	85	20	0	14	1	0	3	5	0	0
Luxembourg	6	2	0	4	1	3	0	0	0	
Netherlands	1900	17	0	280	26	4	140	53	4	8
Malta	2	2	0	31	16	0	7	1	0	0
Poland	3584	966	0	773	6	0	795	7	0	0
Portugal	69	11	0	28	0	0	0	0	0	0
Slovakia	42	5	0	184	7	0	21	1	0	0
Slovenia	127	85	10	14	34	0	24	4	0	10
Sweden	130	14	1	24	11	0	0	0	0	1
UK	21,138	939	43	6,961	5,110	52	531	35	1	96
TOTAL	30757	3148	108	9136	5358	62	3071	507	8	175

No results reported for Germany, Greece, Italy and Spain. No result entered in the original tables for total outbreak column for Luxembourg.

Appendix 4. Timber values – all trees in Great Britain

Lee (S. Lee, FC, *personal communication*, 2003) has made estimates of the volume and value of timber in Great Britain. He has estimated that the volume of standing timber is *ca.* 300 million cubic metres (Table 1). Of this, 25 million is oak (mainly white oaks in England). European beech (*F. sylvatica*) is relatively unimportant outside of England but the total volume of timber is 9 million cubic metres.

Table 1. Volume (m^3) (millions) of timber in standing trees in woodlands and small woods in Great Britain

Species	England	Scotland	Wales	Great Britain
Total conifers	63.5	155.0	32.0	250.5
Oak (mainly white oak)	18.0	1.5	5.5	25.0
European beech	7.5	0.5	1.0	9.0
Other broadleaves	28.5	9.5	4.5	42.5
Total broadleaves	44.0	11.5	10.5	66.0
Total – all species	107.5	166.5	42.5	316.5

The estimated values of the volume of timber for standing trees in Great Britain† (S. Lee, FC, *personal communication*, 2003) detailed in Table 1 is shown in Table 2. These values are derived from estimated values of £6 /m^3 for conifers and £10 /m^3 for broadleaf species giving a derived total value of the timber standing in British forests of £2 billion.

Table 2. Estimated timber value (£ million) of standing trees in woodlands and small woods in Great Britain

Species	England	Scotland	Wales	Great Britain
Total conifers	378.5	926.0	185.0	1490.0
Oak (mainly white oak)	159.0	13.5	23.0	**196.0**
European beech	73.0	5.5	8.5	**87.0**
Other broadleaves	221.5	83.0	17.5	322.5
Total broadleaves	453.0	102.0	48.5	603.5
Total – all species	831.5	1028	233.5	2093.5

Whilst the value of conifer timber is fairly stable, the value of broadleaf species can vary from negative (more expensive to fell than the value of the firewood) to very high in the case of veneer oak (for example).

Assuming a 50-year rotation for conifers and 100-year rotation for broadleaf species these derived figures approximate to an annual value for all species of *ca.* £35 million (19.5, 11.5 and 4 million pounds for Scotland, England and Wales respectively).

In addition to the values given in Table 2 there is a value associated with the individual standing trees which in terms of purely timber value could be between £30m and £80m in total but at roughly £1 to £2 million per year this is a relatively small contribution. (S. Lee, FC, *personal communication*, 2003).

In addition to the estimated value of the timber of standing trees in Great Britain estimates have also been made of the social and environmental value of forests (Willis *et al.*, 2003) as summarised below (S. Lee, FC, *personal communication*, 2003). These include values for

† Other than 122.5 million individual trees in the landscape and excluding private gardens - S. Lee, FC, *personal communication*, 2003.

open access free recreation, landscape amenity, biodiversity and carbon sequestration. Other benefits not presented here include water supply and quality, pollution absorption, health effects and the preservation of archaeological artefacts

Table 3. Annual value (£ million) of some of the social and environmental benefits of forestry in Great Britain

Location	Recreation	Landscape	Biodiversity	Carbon sequestration	Total
England	354	124	363	43	885
Scotland	25	19	19	41	104
Wales	13	7	4	9	34
Total GB	393	150	386	94	**1022**

The social and environmental benefits of British forests are therefore estimated to be *ca*. £1022 million per year. This is made up principally of recreational and biodiversity benefits followed by landscape value and carbon sequestration.

Whilst the estimated annual value of timber is small by comparison (*ca*. £36m) there are obvious benefits in employment related to this raw material as well as the products produced from it.

In crude terms combining the raw timber value and the social and environmental benefits British forests could be valued at *ca.* £1058 million per year (2003 figures).

Lee (S. Lee, FC, Personal Communication, 2003) has attempted to give more detailed illustrations of the social and environmental benefits of three forests in regions of England based upon Willis *et al*., 2003. The values (Table 4) were derived by estimating the percentage of the total value of forests in each region from the estimated percentage area which each of the three forests represents in that region. Timber values for each region were estimated at £2m.

The forests selected were:

1. The New Forest, Hampshire. An area rich in broadleaf species with a high amenity and biodiversity value close to highly populated areas. Represents 35% of the south-east region

2. Grizedale Forest, Cumbria. A forest with a higher proportion of conifers but also with high values for recreation. Represents 40% of the north-west region.

3. Kielder Forest in Northumberland. A large post-war man-made forest, predominately comprised of exotic conifers. Represents 70% of the north-east region

Table 4. Estimated annual value (£ million) of some of the social and environmental benefits of three forests in England

Forest	Recreation	Landscape	Biodiversity	Carbon sequestration	Total
New Forest	32	12	49	4	**97**
Grizedale	14	5	11	2	**32**
Kielder	3	4	13	2	**22**

Appendix 5. Countries for which *Phytophthora ramorum* is on either their regulated pests lists or mentioned in their legislation (prepared by S. Bishop, CSL)

Country	Source	Country	Source	Country	Source
Albania	IPPC 2	Finland	IPPC 1 and 2	Papua New Guinea	IPPC 2
Antigua and Barbuda	IPPC 1 and 2	French Polynesia	IPPC 1 and 2	Paraguay	IPPC 1 and 2
Armenia	IPPC 1	Germany	IPPC 1	Peru	IPPC 1 and 2
Australia	IPPC 1 and 2	Greece	IPPC 1 and 2	Philippines	IPPC 1
Austria	IPPC 1 and 2	Grenada	IPPC 1 and 2	Poland	IPPC 1 and 2
Barbados	IPPC 1	Guinea	IPPC 1	Sabah, East Malaysia	IPPC 1
Belarus	IPPC 1 and 2	India	IPPC 1	Saint Kitts and Nevis	IPPC 1 and 2
Belgium	IPPC 1 and 2	Indonesia	IPPC 1	Saint Lucia	IPPC 2
Benin	IPPC 1	Korea, Republic of	IPPC 2	Saint Vincent and the Grenadines	IPPC 1
Bulgaria	IPPC 1 and 2	Lebanon	IPPC 1	Samoa	IPPC 1
Burundi	IPPC 1 and 2	Madagascar	IPPC 1 and 2	Senegal	IPPC 1
Cambodia	IPPC 1 and 2	Malaysia	IPPC 1	Serbia	IPPC 1 and 2
Cameroon	IPPC 1	Mali	IPPC 1 and 2	Slovenia	IPPC 1 and 2
Canada	EPPO PQR	Malta	IPPC 2	South Africa	IPPC1 and CSL
Chile	IPPC 1 and CSL	Mauritania	IPPC 1 and 2	Sweden	IPPC 1
Cook Islands	IPPC 2	Mauritius	IPPC 1 and 2	FYR Macedonia	IPPC 1 and 2
Costa Rica	IPPC 2	Mexico	EPPO PQR	Turkey	IPPC 1 and 2
Croatia	IPPC 1 and 2	Micronesia, Federated States of	IPPC 1	Ukraine	IPPC 1 and 2
Czech Republic	IPPC 1 and 2	NAPPO members	EPPO PQR	United Kingdom	IPPC 1 and 2
Denmark	IPPC 1	Netherlands	IPPC 1 and 2	USA	EPPO PQR
EPPO members	EPPO PQR	New Zealand	IPPC 1 and 2	Vietnam	IPPC 1 and 2
Ethiopia	IPPC 1	Nigeria	IPPC 1	Yemen	IPPC 1 and 2
EU members states	2000/29/EC	Norway	CSL		

Those EU member states and EPPO countries which are referenced on the International Phytosanitary Portal have been given individual entries in the table. All other EU member states and EPPO countries are covered by the general entries for 'EPPO members' and 'EU members states'.

EPPO (2005) Plant Quarantine Data Retrieval System v4.3, EPPO, Paris.
IPPC 1 (2007) Phytosanitary restrictions, requirements and prohibitions (Art. VII.2b). Available on-line at www.ippc.int last accessed 09/02/07
IPPC 2 (2007) List of regulated pests (Art. VII.2i). Available on-line at www.ippc.int last accessed 09/02/07