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Host species in the context of control of *Phytophthora ramorum*

ANSES opinion
Collective expert appraisal report

December 2018 - Scientific Edition

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Host species in the context of control of *Phytophthora ramorum*

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ANSES Opinion
Request No 2017-SA-0259

The Director General

Maisons-Alfort, 20 December 2018

OPINION
of the French Agency for Food, Environmental and Occupational Health & Safety

on "host species in the context of control of *Phytophthora ramorum*"

On 26 December 2017, the French Directorate General for Food (DGAL) made a formal request to ANSES for an expert appraisal on host species in the context of control of *Phytophthora ramorum*.

1. BACKGROUND AND PURPOSE OF THE REQUEST

Since the early 2000s in Europe, the pathogen *Phytophthora ramorum* (a "pseudo-fungus" belonging to the class Oomycetes, within the Stramenopile lineage) has been known to cause leaf necrosis on ornamental plants, mainly rhododendron and viburnum, in nurseries and semi-natural areas (Werres *et al.*, 2001, Appiah *et al.*, 2004, Xu *et al.*, 2009). At about the same time, it was described as the agent of sudden oak death in California (Garbelotto *et al.*, 2001, Rizzo *et al.,* 2002), where some highly susceptible oak species have developed trunk cankers and died. The situation in Europe changed abruptly in 2009, when an outbreak of *P. ramorum* was described on Japanese larch plantations in Great Britain, associated with needle loss, branch dieback, resin cankers and lastly, massive tree mortality (Brasier and Webber, 2010).

This formal request follows the detection of *P. ramorum* for the first time in France, on Japanese larch (*Larix kaempferi*) in Finistère in May 2017 (Schenck *et al.*, 2018), which was officially notified. *P. ramorum* is classified as a Category 1 health hazard for plant species under French regulations (Ministerial Order of 15 December 2014), and is therefore subject to mandatory control measures.

Larch is an important forest species in France, with natural stands of *Larix decidua* in the Alps and planting areas increasing substantially (Figures 1 and 2). Unlike in Great Britain, European (*L. decidua*) and hybrid (*L. × eurolepis = L. decidua × L. kaempferi*) larch are of major importance as reforestation species (see the Ministry of Agriculture's statistics on plant sales). Hybrid larch is the subject of an INRA improvement programme at Orléans (Lelu-Walter and Pâques, 2009) and several varieties are available in the European (http://ec.europa.eu/forematis/) and French (http://agriculture.gouv.fr/fournisseurs-especes-reglementees-provenances-et-materiels-de-base-forestiers) catalogues. There are also several seed orchards in France.

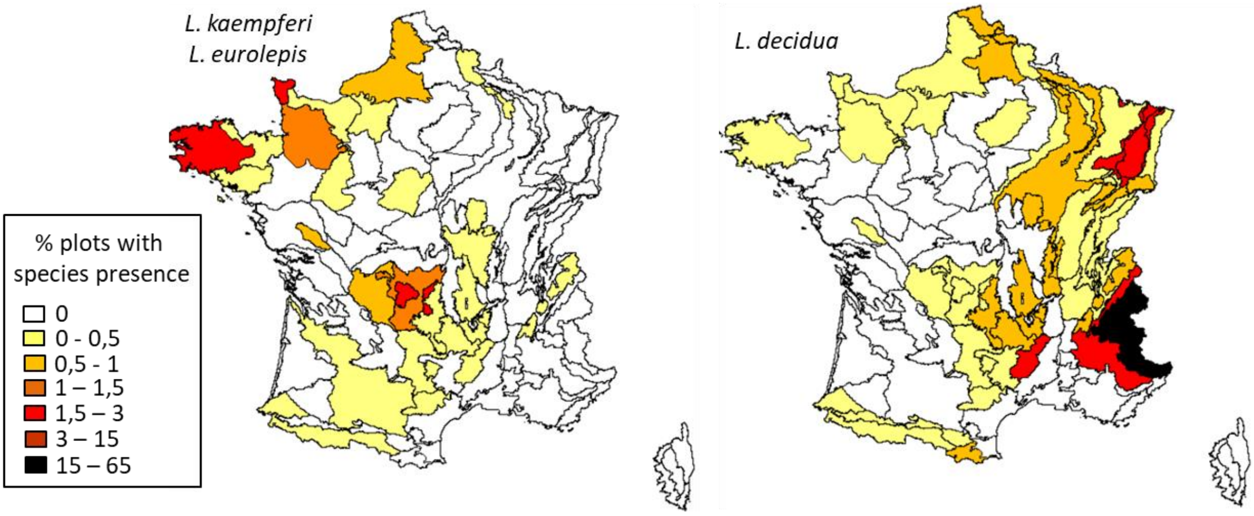


Figure 1: Frequency of larch in surveys by the French National Forest Inventory (IFN) (2005-16). *L. eurolepis* has been grouped together with *L. kaempferi* because this species accounts for less than 0.2% in surveys in all regions.

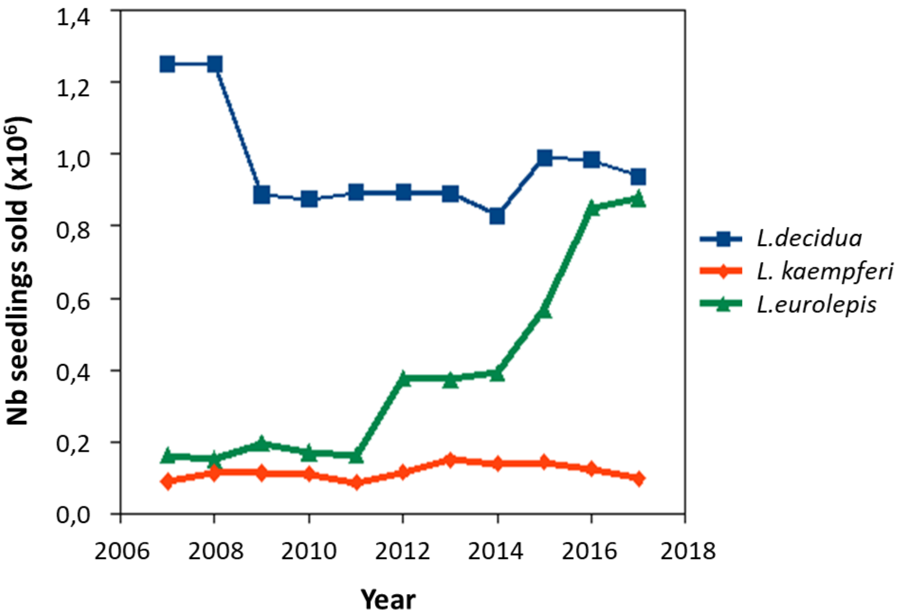


Figure 2: Changes in sales of *Larix* spp. forest seedlings in France (Source: Ministry of agriculture)

Given its broad host range, *P. ramorum* could threaten many forest species besides larch if conditions were to favour its development.

An extract from the text of the formal request letter is provided here to define the purpose of the formal request:

"With a view to improving control strategies against P. ramorum, a literature review is requested on species susceptible to this oomycete, in Europe and in climates similar to those in France, without

neglecting plants from the understory, particularly species of the genera Rhododendron, Viburnum or Vaccinium, or other larch and hybrid larch species.

This study will aim to identify climatic or anthropogenic factors and plant associations that are conducive to the establishment and spread of the pseudo-fungus. Species will then be classified according to their degree of susceptibility and the host type will be identified: foliar, terminal or both. The biological mechanisms and population dynamics will be briefly discussed, as well as exploratory avenues for research. Maps of risk areas for highly and moderately susceptible forest species and of corridors enabling spread will help managers better anticipate and adapt control methods."

2. ORGANISATION OF THE EXPERT APPRAISAL

The expert appraisal was carried out in accordance with French Standard NF X 50-110 "Quality in Expert Appraisals – General Requirements of Competence for Expert Appraisals (May 2003)".

The expert appraisal falls within the sphere of competence of the Expert Committee (CES) on "Biological risks for plant health (RBSV)".

ANSES entrusted the expert appraisal to the Working Group on "*Phytophthora ramorum*". The methodological and scientific aspects of the work were presented to the CES between 20/03/2018 and 13/11/2018. The work was adopted by the CES "RBSV" at its meeting on 13/11/2018.

ANSES analyses interests declared by experts before they are appointed and throughout their work in order to prevent risks of conflicts of interest in relation to the points addressed in expert appraisals. The experts' declarations of interests are made public via the ANSES website (www.anses.fr).

3. ANALYSIS AND CONCLUSIONS OF THE WG AND THE CES

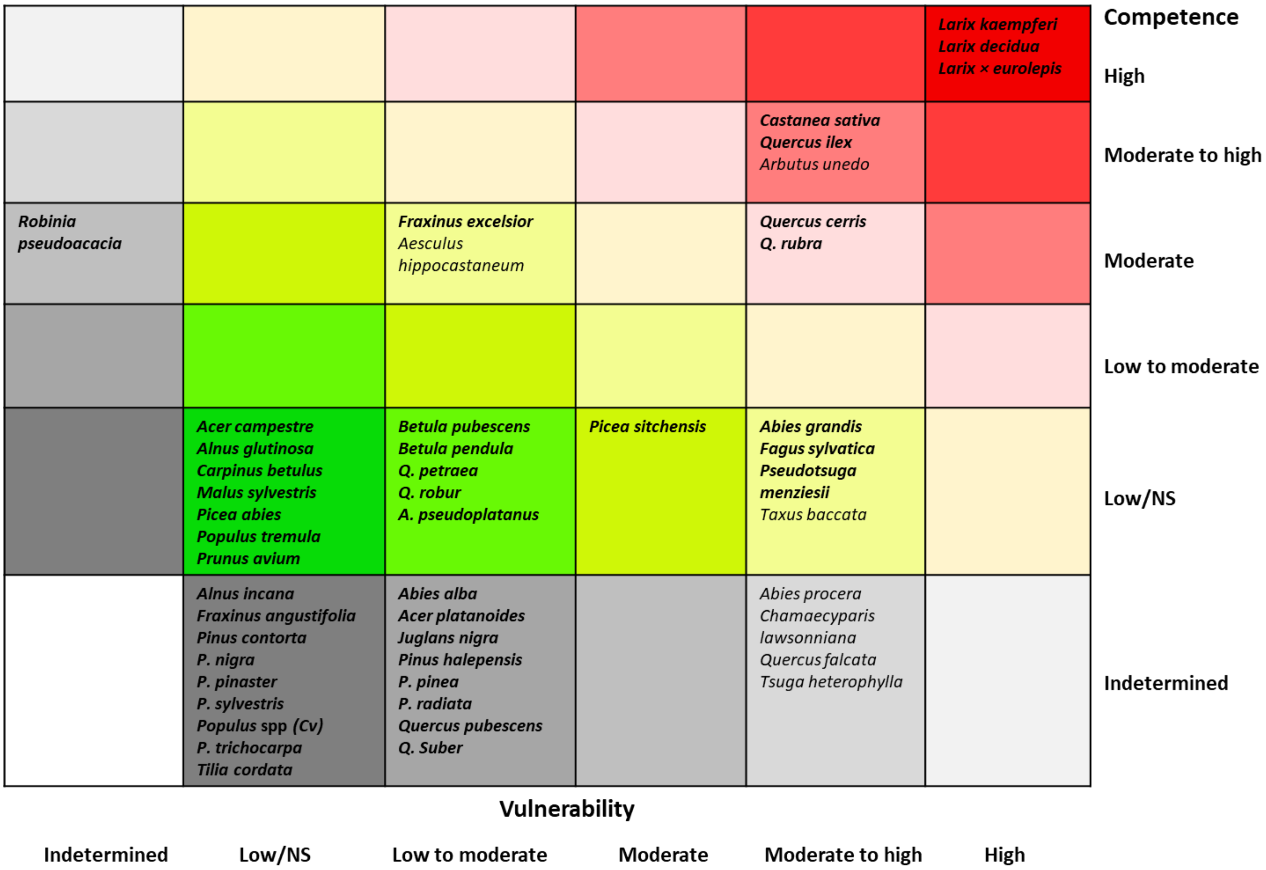
Classification of species susceptibility

The experts proposed a new terminology for classifying species susceptibility, to avoid confusion between types of symptoms and epidemiological role, and ambiguities from terms used differently by different communities of pathologists. The terminology used here differentiates two components of susceptibility: **vulnerability** (related to the expression and severity of symptoms on different organs) and **competence** (related to the epidemiological role of transmission of the pathogen, via its sporulation), which may interact.

Based on the available data, these two components were assessed for the 136 forest tree species in France (including the 66 regulated species) using five rankings from "not significant" to "high". Competence was also assessed for the 47 most common forest shrub species found in French forests. **However, it should be stressed that these assessments were often associated with moderate to high uncertainties**. Lastly, a list of natural ornamental host species of *P. ramorum* was produced (Figure 3).

- At the top of the vulnerability and competence ranking were **the three *Larix* species** *(L. kaempferi, L. decidua, L.* x *eurolepis*), which could not be distinguished from each other after a thorough analysis of all the available data. However, while uncertainty was low concerning *L. kaempferi*, for which the epidemic is proven, it was moderate for the other two species, for which the field data are very incomplete.
- The case of **sweet chestnut** is of great concern. We assessed its vulnerability and competence as moderate to high, but there are still moderate uncertainties. The situation concerning this species has recently changed in Great Britain. If it were confirmed that *P. ramorum* sporulation on sweet chestnut is sufficient to cause multiple auto-infections leading to dieback (with vulnerability increasing to high) and to actively contribute to the pathogen's multiplication and transmission (causing competence to increase to high), the economic and environmental risk posed by *P. ramorum* would be considerably greater given the importance of *Castanea sativa* in France.

- Among the other forest species, some **oaks** (*Quercus ilex, Q. cerris* and *Q. rubra*) have moderate to high vulnerability and moderate or moderate to high competence (for *Q. ilex*), and should therefore be considered with caution. Fortunately, according to current knowledge, sessile and pedunculate oaks have only low to moderate vulnerability and not significant to low competence. **Beech** has higher vulnerability (in the form of trunk cankers) but this can only be expressed in the presence of a high inoculum produced on other competent hosts. Among the conifers, **Douglas fir, Sitka spruce and grand fir** can express relatively severe symptoms (mortality of the current season's growth), but numerous observations in North America and Great Britain have shown that their competence is not significant (examples of "foliar" hosts that do not allow spore-formation). As with beech, therefore, damage is only observed in situations of high inoculum produced by other competent species.
- Lastly, it is necessary to mention a number of species with competence estimated as moderate to high: **ash, black locust (false acacia) and strawberry tree**.



Indetermined	Low/NS	Low to moderate	Moderate	Moderate to high	High	Competence
					Larix kaempferi ***Larix decidua*** ***Larix × eurolepis***	High
				Castanea sativa ***Quercus ilex*** *Arbutus unedo*		Moderate to high
Robinia pseudoacacia		***Fraxinus excelsior*** *Aesculus hippocastaneum*		***Quercus cerris*** ***Q. rubra***		Moderate
						Low to moderate
	Acer campestre ***Alnus glutinosa*** ***Carpinus betulus*** ***Malus sylvestris*** ***Picea abies*** ***Populus tremula*** ***Prunus avium***	***Betula pubescens*** ***Betula pendula*** ***Q. petraea*** ***Q. robur*** ***A. pseudoplatanus***	***Picea sitchensis***	***Abies grandis*** ***Fagus sylvatica*** ***Pseudotsuga menziesii*** *Taxus baccata*		Low/NS
	Alnus incana ***Fraxinus angustifolia*** ***Pinus contorta*** ***P. nigra*** ***P. pinaster*** ***P. sylvestris*** ***Populus spp (Cv)*** ***P. trichocarpa*** ***Tilia cordata***	***Abies alba*** ***Acer platanoides*** ***Juglans nigra*** ***Pinus halepensis*** ***P. pinea*** ***P. radiata*** ***Quercus pubescens*** ***Q. Suber***		*Abies procera* *Chamaecyparis lawsonniana* *Quercus falcata* *Tsuga heterophylla*		Indetermined

Vulnerability

Figure 3: Classification of susceptibility (competence and vulnerability) to *Phytophthora ramorum* of regulated forest tree species in France (in bold) and of a few other unregulated species (NS = not significant). Species for which both components are undetermined have not been included. Many uncertainties are moderate or high, read the text for more details.

Risk mapping

The risk mapping model by Meentemeyer *et al.* (2004), already used in Sansford *et al.* (2009), was chosen because it can integrate the effects of both climate and the competence of vegetation. **Several improvements were made with respect to the work carried out under the European RAPRA project** (Sansford *et al*., 2009) to adapt this model to France, concerning: i) the level of spatial resolution of the meteorological data used, ii) the extension of the score calculation period to cover the whole year in order to take the sporulation period into account (which is different in Europe and the United States), iii) the consideration of relative humidity, and iv) the competence of plant communities in forests (not taken into account in RAPRA due to a lack of data for Europe). It should be pointed out that major **sources of uncertainty** remain regarding the determinants of the risk posed by *P. ramorum*, whether in terms of the ability of woody vegetation to multiply inoculum and enable persistence of the oomycete (competence), or of certain climate components (impact of severe winters on winter survival and on the level of primary inoculum at the beginning of the season). It can also be added that there is genetic and phenotypic diversity in *P. ramorum* (Dodd *et al*., 2015) and varying susceptibility in the host species (Hayden *et al*., 2011; Cobb *et al*., 2018), which will inevitably increase uncertainty in the model predictions.

Despite this, some fairly clear conclusions emerge from this study.

Competence of vegetation

We did not identify any understory woody plants with high competence and high regional frequency that might play the same epidemic role as California bay laurel in the western United States or rhododendron (*Rhododendron ponticum*) in Great Britain (Purse *et al*., 2013). Rhododendron are generally rare in French forests. There are areas in the eastern Languedoc (Gard) and in Corsica where the frequency of holm oak, sweet chestnut, strawberry tree, *Viburnum tinus* and *Rhamnus alaternus* gives the vegetation high competence, but the climate in these areas is not favourable to *P. ramorum*. The Alpine larch forest is another area with high vegetation competence. Our study confirmed RAPRA's conclusions on this point: the climate of this area is not very favourable to *P. ramorum*. **For the rest of France, the average vegetation competence is moderate**. **However, this result must be placed in perspective**:

(i) Sweet chestnut was identified as a forest species at risk of *P. ramorum* outbreaks (Denman *et al*., 2005b, Webber *et al*., 2017). Indeed, sweet chestnut stands far away from other inoculum sources such as larch or rhododendron have been affected in southern Britain and are dying back from year to year, suggesting that this species may have significant competence. In Great Britain, sweet chestnut is relatively uncommon (fewer than 20,000 ha in 2000; Braden and Russell, 2001), especially in areas favourable to *P. ramorum*. However, in France, sweet chestnut is the fourth most common deciduous species for standing timber volume (5% of the French total) with more than 700,000 hectares (IFN 2014 *La forêt en chiffres et en cartes* [The forest in figures and maps]). Sweet chestnut is common in areas with a climate favourable to *P. ramorum* such as Brittany, Limousin, Montagne Noire, the Pyrenean foothills, Cévennes and eastern Isère. Underestimating the competence of sweet chestnut would have serious consequences on our conclusions. This is probably the major risk in our country, but still with a high level of uncertainty.

(ii) Competence maps represent an average situation, with values interpolated using IFN sampling data. They do not therefore provide information on any possible local risk associated with the existence of stands with high competence and high vulnerability such as Japanese larch.

(iii) The vegetation competence maps produced only concern forest stands. Knowledge of the frequency of plant species outside forests is too limited to allow further analysis. In particular, it is clear that there is inadequate knowledge of hedges and highly anthropised environments such as parks and gardens, which could play a significant role when they are close to forests. For sweet chestnut, orchard data should also be taken into account.

Areas with a favourable climate

Our study enabled predictions to be refined on areas of France with a favourable climate for the development of *P. ramorum*, compared to previous studies (Figure 4). The use of meteorological data with a finer spatial resolution than that used in RAPRA enabled better consideration of hydric parameters (precipitation, relative humidity), which have a decisive role in the epidemiology of *P. ramorum*. On the other hand, the Meentemeyer model had to be adapted to take into account the sporulation period of *P. ramorum*, which is different in Europe compared to North America.

These changes led to large differences for areas favourable to *P. ramorum* in France compared to what was indicated in RAPRA with the same model. **In addition to western France (Brittany, Limousin, Pyrenean foothills) and the coastal area along the Channel, many medium altitude areas appear to be climatically favourable to *P. ramorum*, in the south (Montagne Noire, Cévennes) and in the east (Vosges and Jura)**. While the mountainous massifs of Eastern France do not include vegetation with high competence, this is not the case in the Montagne Noire and Cévennes, where the significant presence of sweet chestnut makes the situation problematic. According to the DSF's "plantation" survey, the areas where larch is planted in France generally have a climate favourable to *P. ramorum*. The Mediterranean area seems to be unfavourable to the development of *P. ramorum*, contrary to what might be suggested from rough "climate matching" projections with California (Sansford *et al*., 2009).

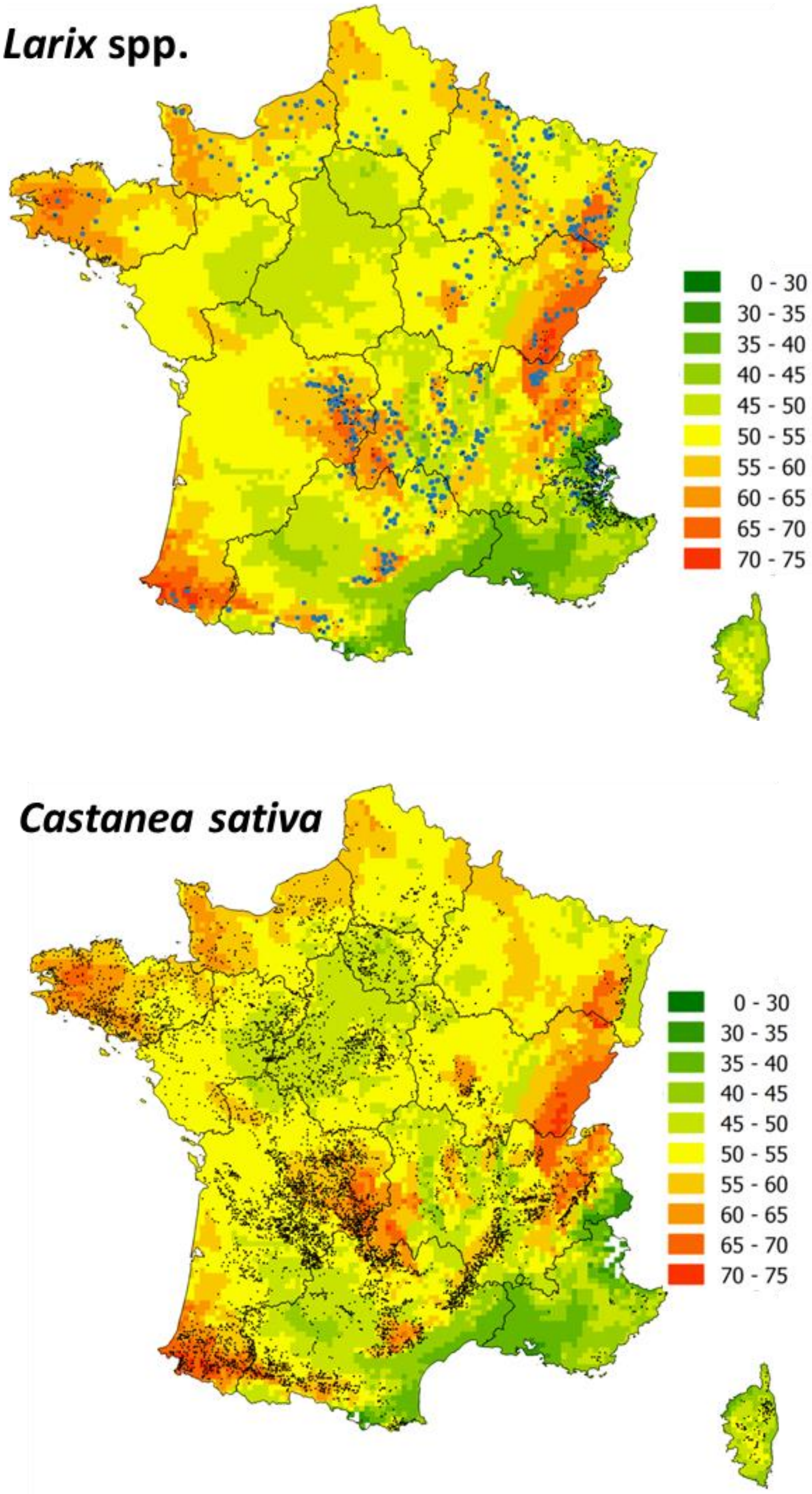


Figure 4: Location of *Larix* spp. and *Castanea sativa* (black dots = IFN data, 2005-2016) on the climate risk map. The blue squares on the *Larix* spp. map represent the locations of larch plots in the DSF's "plantation" surveys (2006-17).

Synopsis: what scenario would lead to an outbreak situation?

The analysis of recent epidemics caused by *P. ramorum* in the United States and Europe (United Kingdom and Ireland) shows a certain level of unpredictability, due to accidental introductions and the ability of this pathogen to adapt to numerous hosts and environments. However, some common characteristics make it possible to develop a **"most plausible scenario" leading to these outbreak situations, with three main stages**:

(1) Accidental introduction and transport of *P. ramorum* via plant trade, particularly rhododendron and other ornamental species;
(2) Multiplication in semi-natural or natural environments, particularly forests, on highly competent hosts such as California bay laurel or *Rhododendron ponticum*;
(3) Outbreaks on forest trees, whose expansion is determined by the presence of susceptible hosts (high vulnerability and competence) and favourable climatic conditions.

This scenario is supported by a number of genetic and epidemiological studies (Xu *et al*., 2009; Chadfield and Pautasso, 2012; Croucher *et al*., 2013; O'Hanlon, 2016).

It can be hypothesised that the successive and increasingly frequent appearance (detection) of *P. ramorum,* first on ornamental plants in nurseries, then on shrubs (related to ornamental species or varieties) in forests and finally on forest trees, corresponds to a gradual increase and diversification of its population, becoming increasingly free from the anthropised environments favourable to its establishment and multiplication. This dynamic, accompanied by a lag phase of varying length between its presence in a controlled environment (e.g. gardens) and its escape into the wild, is typical of many invasive alien species, including plants (Sakai *et al.*, 2001). An important point in this dynamic is that the spatial expansion observed in the natural environment can be very rapid after the initial reports in that environment, strongly affecting the chances of successful eradication (Hansen *et al*., 2008; Harwood *et al.*, 2009; Parnell *et al*., 2010; Cunniffe *et al*., 2016). Several reasons explain the speed of the epidemic: multiple introductions, which are a consequence of the species' demographic dynamics (exponential start), under-sampling (no systematic surveillance before the first reports, which are only the tip of the iceberg, with other small epidemics possibly going unnoticed) (Filipe *et al.*, 2012), an increase in long-distance dispersal events with the population size (Croucher *et al*., 2013), adaptive phenomena in the invasive species over time (Sakai *et al*., 2001; Croucher *et al*., 2013; Robin *et al*., 2017), and the very high susceptibility of naïve hosts, i.e. those never before confronted with the pathogen (Garbelotto and Hayden, 2012). This rapid expansion can be illustrated by the case of Scotland, where the first outbreak of *P. ramorum* was observed on larch in November 2010, during surveillance missions following its discovery in England. After two autumns and winters regarded as favourable (rainy and mild) in an area of extensive larch stands, 5000 to 6000 ha were infected in 2013 (Forestry Commission Scotland website).

It can be seen that the outbreaks in larch plantations in the Sizun area of Brittany (Finistère) seem to correspond closely to this general scenario (Figure 5). Indeed, they are located in a high-risk area, which combines both a high density of rhododendron production nurseries with early reports of *P. ramorum* detection (each year since 2002), the highest density of rhododendron in French forests (even if its abundance remains relatively low), detections of *P. ramorum* on rhododendron in forest areas (since 2007, in Finistère and Morbihan, DSF database, although this presence has not been confirmed by subsequent sampling in the same area), a favourable climate and the presence of Japanese larch. The high-risk area in the Alps corresponds to the presence of particularly competent hosts (larch, sweet chestnut), but this must be weighed against the fact that the climate here is not favourable to *P. ramorum*.

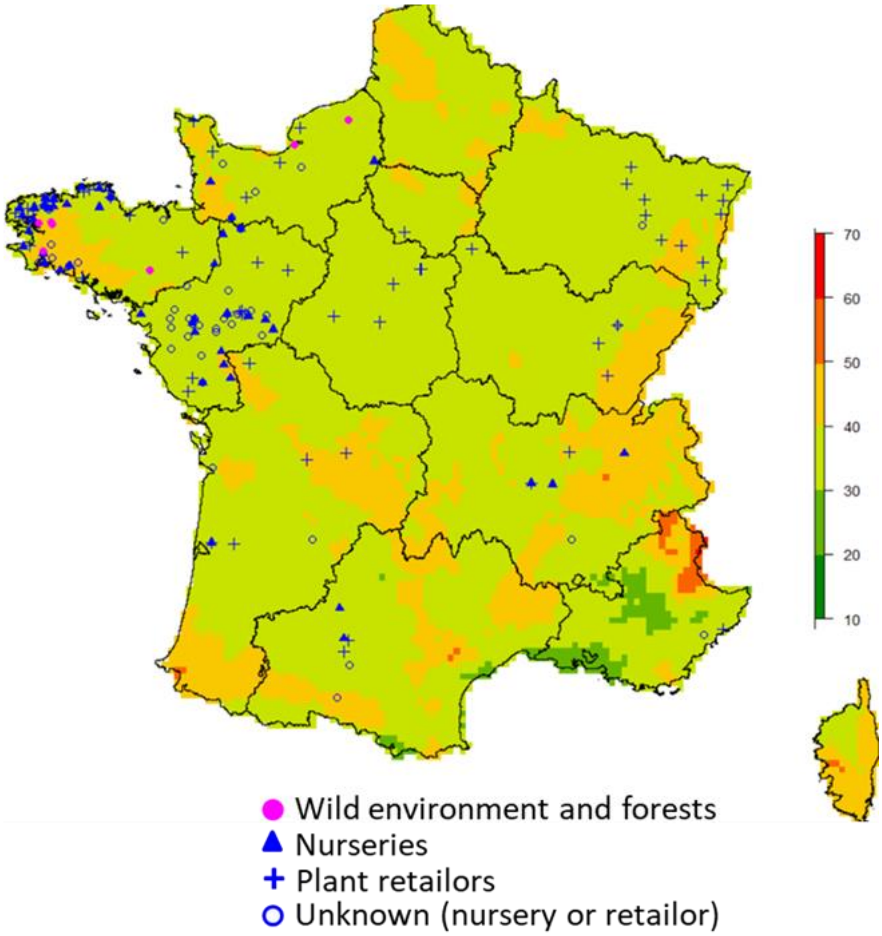


Figure 5: Location of the identified points where *P. ramorum* is present in France on the *P. ramorum* risk map, integrating climatic variables and competence (map created with the 95% quantile of the competence map)

Recommendations

Practical recommendations

Eradication

According to the scenario described above, management of the "Brittany outbreak" is of paramount importance. Based on the British experience, DSF surveillance over the past few years gives reason to hope that one of the first outbreaks in the forest environment has been detected in a phase where disease progression is still slow. Moreover, given the relatively low abundance of rhododendron in the forest, epidemic relays are limited. Unlike the British case, therefore, eradication is a possibility, by eliminating not only larch but also "wild" rhododendron in the affected area. The invasive alien species status of *R. ponticum* in Brittany and its epidemic role for *P. ramorum* justify taking measures to eliminate this species in forests before it reaches population levels comparable to those in the United Kingdom. Eradication procedures should also be accompanied by hygiene measures to limit the spread of *P. ramorum* via tools, vehicles, technical staff and inspectors. The spread of *P. ramorum* by logs from infected trees is unlikely. Indeed, Davidson *et al.* (2005, 2008) showed that *P. ramorum* sporulation was not observed from intact bark of *Quercus* sp. or *Notholithocarpus densiflorus*. Sporulation from *N. densiflorus* was only observed on the bark of small diameter stems (<5 cm, chlamydospores and sporangia) or large-diameter wounded stems (chlamydospores only, when the phloem was exposed). On this basis, the British do not take any special precautions when transporting infected larch logs, but treat them separately in "approved" sawmills where the logs are debarked and the bark composted (Forestry Commission website).

In addition to eradication measures, it would be advisable to develop information campaigns aimed at the public, forest owners and professionals, as has been done in the Netherlands for example (de Gruyter and Steegs, 2006). Alexander and Lee (2010) also stressed the importance of information campaigns/mobilisation of all the parties in California.

Forest surveillance

Aside from the outbreak, very detailed surveillance of the **Brittany** area on larch, rhododendron and sweet chestnut is highly recommended. In order of priority, the intensity of surveillance should then focus on the **Normandy and Limousin** regions. The first combines larch plantations, relatively favourable climate and competence and detection of *P. ramorum* in nurseries and for the first time in the wild on rhododendron in 2007 (Calvados) and then again in 2014 (Seine Maritime) (N. Schenck, LNPV-MAF Report, 2007; detections not confirmed by subsequent sampling in the same areas). Limousin is strongly concerned due to its larch plantations, particularly *L. kaempferi*, and also has rather favourable climate and competence. More generally, special attention should be paid to all larch plantations (regardless of species) in areas with a climate favourable to *P. ramorum* and **any suspicion regarding sweet chestnut** should be investigated by screening for *P. ramorum*. The use of rapid field immunological tests (Pocket Diagnostic® LFD test, a registered trademark of Abingdon Health, UK), specific to the genus *Phytophthora* and applicable to leaves or branches is particularly interesting in this regard because it enables more effective targeting of samples to be sent to the laboratory for validation and species identification.

Nursery surveillance

The role of the plant trade from and between nurseries in the spread of plant pathogens, especially *Phytophthora* and particularly *P. ramorum*, is now very well established (Jung *et al*., 2016; Liebhold *et al*., 2012; Migliorini *et al*., 2015). This applies not only to forest plants but also, and sometimes even more so, to ornamental plants, as clearly illustrated by the case of *P. ramorum*. This raises the question of regulatory changes aimed at prohibiting imports of certain species whose risk/benefit ratio is too high (https://www.iufro.org/science/divisions/division-7/70000/publications/montesclaros-declaration/). For instance, *Notholithocarpus densiflorus* and *Umbellularia californica* are in the French nursery catalogue.

Checks of nurseries, garden centres, parks and gardens, especially in areas with a favourable climate and environment for *P. ramorum*, are of paramount importance and must be improved. Upstream, good practices to limit the risks of contamination of plant material and substrates by *P. ramorum* should be promoted in nurseries, avoiding the use of fungicidal treatments that only mask symptoms. Different types of approaches are possible, either following a traditional approach (a reactive method based on inspections of control points and material produced) or a systems approach (a proactive method based on the implementation of procedures and audits, and prevention, Parke and Grunwald, 2012).

Many studies have highlighted the diversity of *Phytophthora* spp. communities in nurseries, and the main control points from which samples should be taken are now known: in fact, the entire production chain and all inputs are involved (Parke and Grunwald, 2012). It seems essential to test not only plants with leaf necrosis but also asymptomatic plants, since *P. ramorum* can cause latent infections (Migliorini *et al*., 2015). The list of species to be monitored should be updated regularly based on knowledge of susceptible species. Following any positive detections, it is imperative to implement strict eradication measures on outbreaks in these sites and to verify their effectiveness.

Surveillance of nurseries, garden centres and non-forest environments should be carried out according to an effective sampling and data collection plan. Quality surveillance data (on presence and absence) that are georeferenced, validated and incorporated into databases built according to standard practices are necessary for any epidemiological work. A database meeting these criteria is already available for observations concerning forests that are the responsibility of the DSF. However, data on nursery surveillance have been more difficult to obtain and do not meet the criteria outlined above, despite this being a crucial area for surveillance and therefore management of forest pathogens. Lastly, this still leaves all the private spaces (parks, gardens) or spaces outside forests (non-forested areas, avenue trees, hedges, orchards, etc.) that can act as relays for the infection of forest trees, and for which data are extremely partial or non-existent.

Reforestation in risk areas

Larch plantations, particularly those with hybrid larches, are currently becoming more and more widespread. Although it has not been fully demonstrated that the susceptibility of European and hybrid larch (especially for the marketed varieties) is as high as that of Japanese larch, caution should be exercised and the risk associated with *P. ramorum* should be taken into account more than ever, especially in areas identified as having a favourable climate. According to the current state of knowledge, the creation in these areas of large stands of hosts with proven susceptibility seems risky.

In general, our classification for species susceptibility is consistent with the Forestry Commission's recommendations for planting in risk areas. Thus, among the 13 regulated species in France that we believe have moderate to high vulnerability and/or competence, 10 are considered "at risk" or even to be avoided (for the three species of larch), while the other three are not or are only rarely planted in Great Britain.

Knowledge gaps – Research questions

The level of susceptibility of **European and hybrid larch**, particularly of the marketed varieties (forest reproductive material = FRM), of parents used in seed orchards, or of other material included in the plant breeding programme, has not been characterised. It would be highly desirable to assess this material's susceptibility, under containment conditions and/or in collaboration with Great Britain under natural *P. ramorum* inoculum conditions.

Concerning species susceptibility, the greatest unknown concerns **sweet chestnut**, whose levels of competence (ability to promote *P. ramorum* sporulation) and vulnerability (development of multiple infections, extension from leaves to branches, etc., potentially leading to dieback) remain to be determined, following the observations in Great Britain (Webber *et al*., 2017).

Lastly, several questions remain concerning **the epidemiology of *P. ramorum* in the wild**. In particular, additional studies seem to be needed to gain a better understanding of the oomycete's latency and survival capacity in the environment (particularly in litter), especially from one season to the next, as well as the effect of winter temperatures, potential woody reservoirs and the spatio-temporal dynamics of the inoculum, including vertical propagation to tree crowns, "long-distance" dispersal, etc. *P. ramorum* should be screened for in all ecosystem compartments in the affected area in Brittany. The genetic study of available isolates (and possibly any others that may be obtained in the future), with resequencing of large areas of the genome (for which a version is already available, Tyler *et al*., 2006) could enable the history of the invasion to be reconstructed, in particular to test the scenario of transition from nurseries to wild hosts and then to larch.

4. AGENCY CONCLUSIONS AND RECOMMENDATIONS

The French Agency for Food, Environmental and Occupational Health & Safety endorses the conclusions of the WG and the CES, and recommends:

(i) Carrying out intensive surveillance in forests in Brittany as a priority, to identify any possible new outbreaks of *P. ramorum*, and then in other regions that are climatically favourable to the development of the oomycete (Normandy, Limousin, etc.) where significant densities of vulnerable and competent species are planted (particularly larch and sweet chestnut);

(ii) In the event that *P. ramorum* is detected in a forest, taking eradication measures with regard to infected forest species including understory species such as *Rhododendron ponticum*;

(iii) Stepping up checks of ornamental nurseries and garden centres in order to prevent any new introduction of *P. ramorum* from ornamental host species in France and the European Union;

(iv) Implementing checks of forest nurseries, prioritising those located near forest areas or nurseries infected by *P. ramorum*, to ensure the phytosanitary quality of planting material, especially for species of the genera *Larix* and *Castanea*;

(v) Avoiding planting the three larch species in areas climatically favourable to the development of *P. ramorum*;

(vi) Implementing communication measures aimed at park and garden owners to raise their awareness of the risk of uncontrolled introduction of *P. ramorum* through plants-for-planting from oomycete-infected areas (Brittany and Great Britain);

(vii) Conducting research to resolve uncertainties, in particular regarding the epidemic role of sweet chestnut, and to assess the sensitivity to climate change of the development of the pathogenicity of *P. ramorum*.

Dr Roger Genet

KEYWORDS

Phytophthora ramorum, mélèze, *Larix,* sensibilité, zonage de risque, pépinières, France
Phytophthora ramorum, Larch*, Larix*, susceptibility, risk mapping, nursery, France

Formal request relating to host species in the context of control of *Phytophthora ramorum*

Request No 2017-SA-0259 PHYRAM

Collective Expert Appraisal
REPORT

Expert Committee on "Biological risks for plant health"

Working Group on "*Phytophthora ramorum*"

November 2018

French Agency for Food, Environmental and Occupational Health & Safety,
14 rue Pierre et Marie Curie, 94701 Maisons-Alfort Cedex
Telephone: +33 (0)1 49 77 13 50 - Fax: +33 (0)1 49 77 26 26 - www.anses.fr
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Key words

Phytophthora ramorum, mélèze, *Larix,* sensibilité, zonage de risque, pépinières, France
Phytophthora ramorum, Larch*, Larix*, susceptibility, risk mapping, nursery, France

Presentation of the participants

PREAMBLE: The expert members of the Expert Committees and Working Groups or designated rapporteurs are all appointed in a personal capacity, *intuitu personae*, and do not represent their parent organisation.

WORKING GROUP

Chair

Ms Marie-Laure DESPREZ-LOUSTAU – Research Director, INRA Bordeaux, Ecology of forest tree diseases

Members

Ms Cécile ROBIN – Research Director, INRA Bordeaux, Ecology of forest tree diseases

Mr Renaud IOOS – Head of Unit, ANSES, Mycology and molecular detection

Mr Benoit MARÇAIS – Research Director, INRA Nancy, Epidemiology of forest tree diseases

Mr Marco PAUTASSO – Scientific Coordinator, EFSA, Forest pathology

…………………

EXPERT COMMITTEE

The work covered in this report was monitored and adopted by the following Expert Committee (CES):

- CES on "Biological risks for plant health"

Chair

Mr Thomas LE BOURGEOIS – Research Director, CIRAD, Weed science

Members

Ms Marie-Hélène BALESDENT – Research Director, INRA, Mycology

Ms Françoise BINET – Research Director, CNRS, Functional ecology

Mr Antonio BIONDI – Researcher, University of Catania, Entomologist

Mr Philippe CASTAGNONE – Research Director, INRA, Nematology

Mr Christophe CLEMENT – Professor, University of Reims, Plant biology and physiology

Ms Péninna DEBERDT – Researcher, CIRAD, Phytopathology

Mr Nicolas DESNEUX – Research Director, INRA, Ecotoxicology

Ms DESPREZ LOUSTAU – Research Director, INRA, Mycology

Mr Abraham ESCOBAR-GUTIERREZ – Research Director, INRA, Agronomy

Mr Laurent GENTZBITTEL – Professor, ENSAT, Genetics of plant-microorganism interactions

Mr Hervé JACTEL – Research Director, INRA, Forest entomology

Mr David MAKOWSKI – Research director, INRA, Agronomy

Mr Arnaud MONTY – Professor, University of Liège, Ecology of invasive plants

Ms Maria NAVAJAS – Research Director, INRA, Acarology

Mr Xavier NESME – Research Engineer, INRA, Bacteriology

Mr Stéphan STEYER – Scientific Adviser, CRA-W, Virology

Mr Éric VERDIN – Research Engineer, INRA, Virology

Mr François VERHEGGEN – Professor, University of Liège, Entomology

Mr Thierry WETZEL – DLR Rheinpfalz, Institute of Plant Protection, Virology

…………………

ANSES PARTICIPATION

Scientific coordination

Ms Pauline de JERPHANION – Project Leader – ANSES

Mr Xavier TASSUS – Scientific Expert Appraisal Coordinator – ANSES

CONTRIBUTIONS FROM OUTSIDE THE GROUPS

Larch genetic improvement programme; Mr Luc PAQUES – Research Director – INRA

Susceptibility of Douglas fir to *Phytophthora ramorum;* Mr Matteo GARBELOTTO – Adjunct-Professor – University of California

Phytophthora ramorum epidemic in Great Britain on larch and sweet chestnut; Ms Joan WEBBER – Researcher – Forestry Commission

Phytophthora ramorum epidemic in Great Britain on larch and sweet chestnut; Mr Clive BRASIER – Researcher – Forestry Commission

Phytophthora ramorum epidemic in Great Britain on larch and sweet chestnut; Mr Mick BIDDLE – Inspector – Forestry Commission

CONTENTS

Acronyms and abbreviations

ANSES: French Agency for Food, Environmental and Occupational Health & Safety
DGAL: French Directorate General for Food
DEFRA: UK Department for Environment, Food and Rural Affairs
DSF: French Forest Health Department
ha: hectare
IFN: French National Forestry Inventory
LFD: lateral flow device (immunoassay)
LNPV: ANSES Plant Health Laboratory
MAF: French Ministry of Agriculture and Forestry
FRM: Forest reproductive material
EPPO: European and Mediterranean Plant Protection Organisation
EU: European Union

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1 Background, purpose and procedure for carrying out the expert appraisal

1.1 Background

Since the early 2000s in Europe, the pathogen *Phytophthora ramorum* (a "pseudo-fungus" belonging to the class Oomycetes, within the Stramenopile lineage) has been known to cause leaf necrosis on ornamental plants, mainly rhododendron and viburnum, in nurseries and semi-natural areas (Werres *et al.*, 2001, Appiah *et al.*, 2004, Xu *et al.*, 2009). At about the same time, it was described as the agent of sudden oak death in California (Garbelotto *et al.*, 2001, Rizzo *et al.,* 2002), where some highly susceptible oak species have developed trunk cankers and died. The situation in Europe changed abruptly in 2009, when an outbreak of *P. ramorum* was described on Japanese larch plantations in Great Britain, associated with needle loss, branch dieback, resin cankers and lastly, massive tree mortality (Brasier and Webber, 2010).

This formal request follows the detection of *P. ramorum* for the first time in France, on Japanese larch *(Larix kaempferi*) in Finistère (western part of Brittany) in May 2017 (Schenck *et al.*, 2018), which was officially notified. *P. ramorum* is classified as a Category 1 health hazard for plant species under French regulations (Ministerial Order of 15 December 2014), and is therefore subject to mandatory control measures.

Larch is an important forest species in France, with natural stands of *Larix decidua* in the Alps and planting areas increasing substantially (Figures 1 and 2). Unlike in Great Britain, European *(L. decidua*) and hybrid *(L.* × *eurolepis* = *L. decidua* × *L. kaempferi*) larch, rather than Japanese larch (*L. kaempferi*) are of major importance as reforestation species (see the Ministry of Agriculture's statistics on plant sales). Hybrid larch is the subject of a genetic improvement programme at INRA Orléans (Lelu-Walter and Pâques, 2009) and several varieties are available in the European (http://ec.europa.eu/forematis/) and French (http://agriculture.gouv.fr/fournisseurs-especes-reglementees-provenances-et-materiels-de-base-forestiers) catalogues. There are also several seed orchards in France.

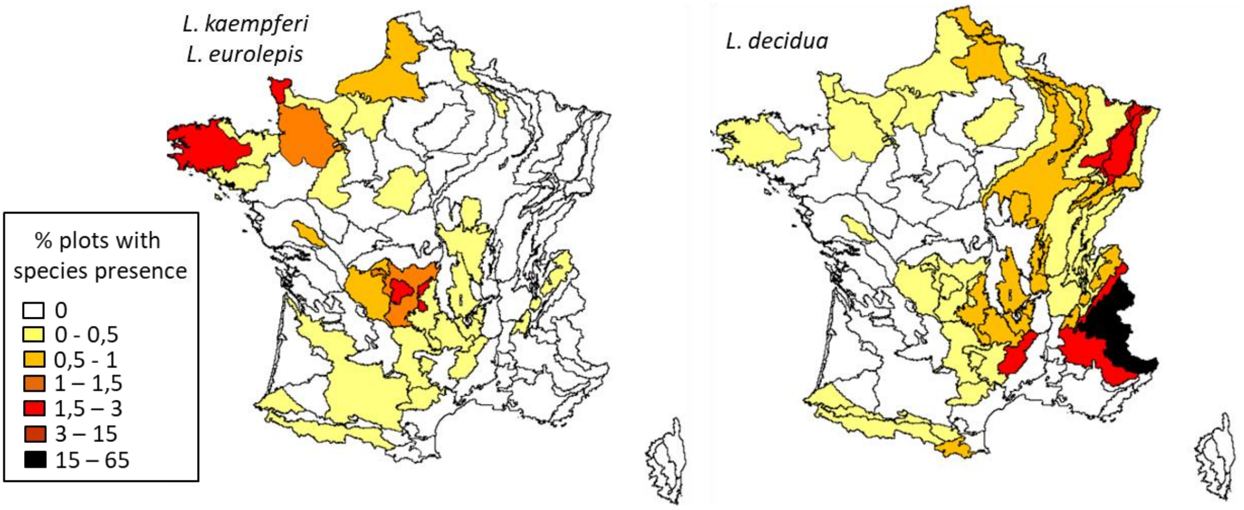


Figure 1: Frequency of larch in surveys by the French National Forest Inventory (IFN) (2005-16). *L. eurolepis* has been grouped together with *L. kaempferi* because this species accounts for less than 0.2% in surveys in all regions

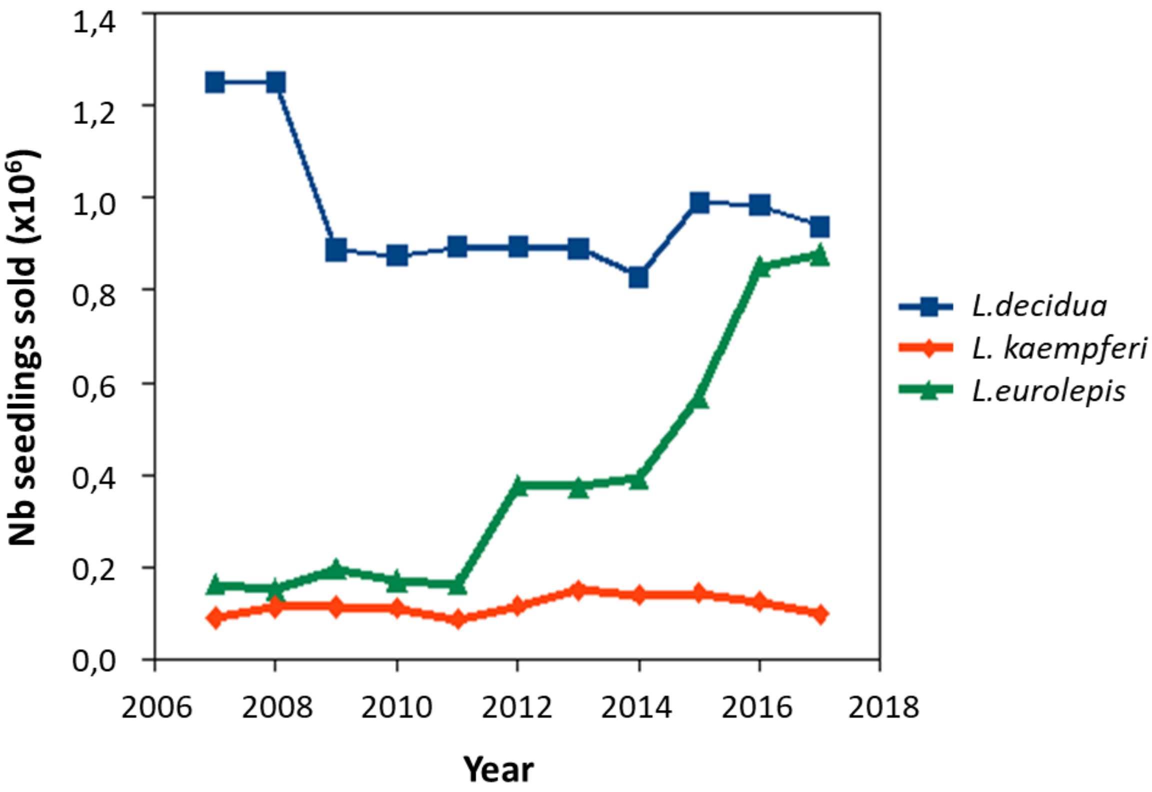


Figure 2: Changes in sales of *Larix* spp. forest seedlings in France (Source: Ministry of Agriculture *DGPE/SDFCB)*

Given its broad host range, *P. ramorum* could threaten many forest species besides larch if conditions were to favour its development.

1.2 Purpose of the request

An extract from the text of the formal request letter is provided here:

"With a view to improving control strategies against P. ramorum*, a literature review is requested on species susceptible to this oomycete, in Europe and in climates similar to those in France, without neglecting plants from the understory, particularly species of the genera* Rhododendron*,* Viburnum *or* Vaccinium*, or other larch and hybrid larch species.*

This study will aim to identify climatic or anthropogenic factors and plant associations that are conducive to the establishment and spread of the pseudo-fungus. Species will then be classified according to their degree of susceptibility and the host type will be identified: foliar, terminal or both. The populations' biological or dynamic mechanisms will be briefly discussed, as well as exploratory avenues for research. Maps of risk areas for highly and moderately susceptible forest species and of corridors enabling spread will help managers better anticipate and adapt control methods."

1.3 Procedure: means implemented and organisation

ANSES entrusted examination of this request to the Working Group on "*Phytophthora ramorum*" reporting to the CES on "Biological risks for plant health".

The methodological and scientific aspects of this group's work were regularly submitted to the CES. The report produced by the Working Group takes account of the observations and additional information provided by the CES members.

This work was therefore conducted by a group of experts with complementary skills. External contributions were also sought on specific points, particularly concerning the situation in England, which was visited by ML Desprez-Loustau, B Marçais and C Robin.

The expert appraisal was carried out in accordance with French Standard NF X 50-110 "Quality in Expert Appraisals – General Requirements of Competence for Expert Appraisals (May 2003)".

1.4 Prevention of risks of conflicts of interest

ANSES analyses interests declared by experts before they are appointed and throughout their work in order to prevent risks of conflicts of interest in relation to the points addressed in expert appraisals.

The experts' declarations of interests are made public via the ANSES website (www.anses.fr).

2 Presentation of the pathogen

2.1 Description

Phytophthora ramorum was formally described for the first time as an agent of twig blight on ornamental plants, mainly rhododendron and viburnum, in nurseries in Germany and the Netherlands (Werres *et al.*, 2001). Characteristic symptoms on rhododendron are black discolouration and mortality of stem tips, and the presence of brown spots on the leaves (especially at the tip) (Figure 3). Within the genus *Phytophthora*, the new species is morphologically characterised by abundant chlamydospore production and the formation of elongated, ellipsoid, caducous sporangia with a short pedicel, similar to those of *P. palmivora*, but of the semi-papillate type. Chlamydospores are much larger and cardinal temperatures much lower (growth from 2 to 26-30°C, with optimum around 20°C) than for *P. palmivora*. The isolates initially studied were all A1 type, which proved to be the case for all isolates subsequently identified in Europe (see below). The ITS1 and ITS2 sequences do not correspond to any previously-described species, and are closest to those of *P. lateralis*, with three and eight different nucleotides respectively. This very close proximity has been confirmed in more recent phylogenetic studies including several genes, which place both of them in clade 8, subclade 8C (Yang *et al.*, 2017).

In the same year that it was formally described on rhododendron, *P. ramorum* was identified as the causal agent of sudden oak death (SOD), which had been present in California since 1994 (Garbelotto *et al.*, 2001, Rizzo *et al.*, 2002). This disease is characterised by the presence of bleeding cankers on oak trunks (*Notholithocarpus densiflorus*, *Quercus agrifolia*, *Q. kelloggii*, *Q. parvula* var. *shrevei*), which can extend to a height of several metres or even tens of metres, preceding the leaf dieback symptoms.

Since this simultaneous descriptions, the species has been reported many times on both continents (Figure 4). In most European countries and in the eastern United States, reports concern nursery plants (with also some cases outside nurseries in parks and gardens). Forestry reports are restricted to California and Oregon for the United States, and the United Kingdom and France for Europe. There are a few other infrequent reports in the wild, in the south-eastern United States from leaf baiting in streams near infected nurseries (Ireland *et al.*, 2013) or in sweet chestnut grove soil in Italy from confirmed metabarcoding in two successive years (Vannini *et al.*, 2012).

Figure 3: *Phytophthora ramorum* symptoms on larch and rhododendron in south-west England (Photos: ML Desprez-Loustau). Left: large necrotic phloem lesions on the trunk of a felled declining larch tree, with positive *Phytophthora* test (bottom test, "T" line, the "C" line is for "Control"; the top test on needles is negative here). Top right: typical symptoms on needles, with grey-purple colouration. Bottom right: infected rhododendron shoot with blackened leaves and shoot tip).

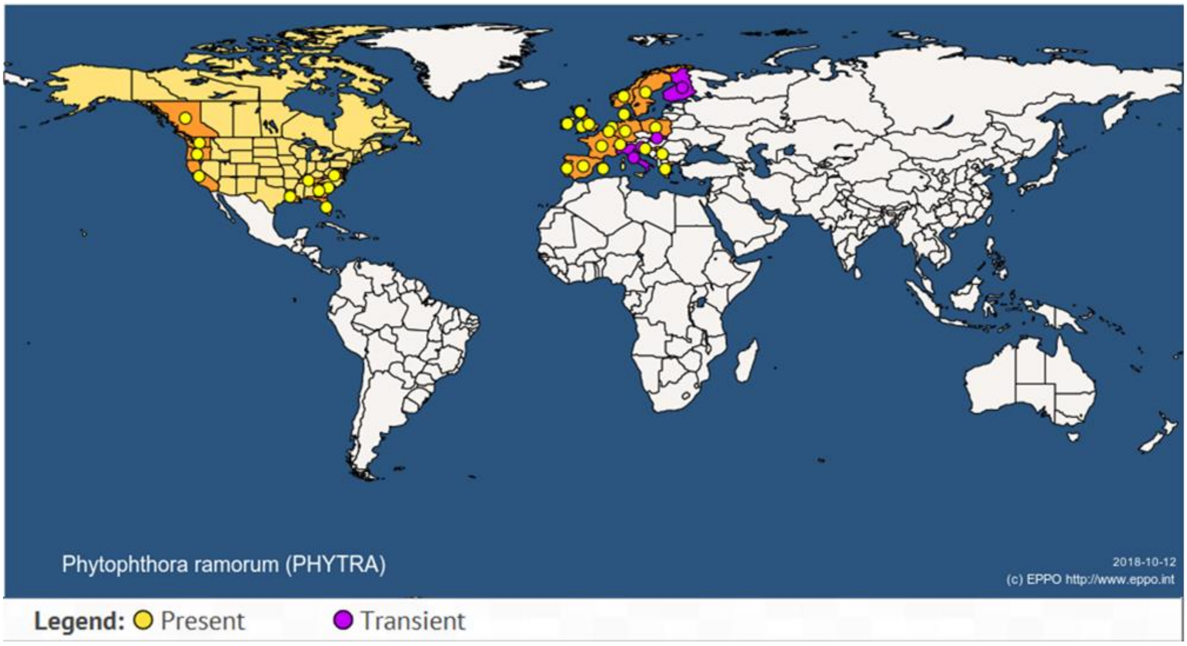
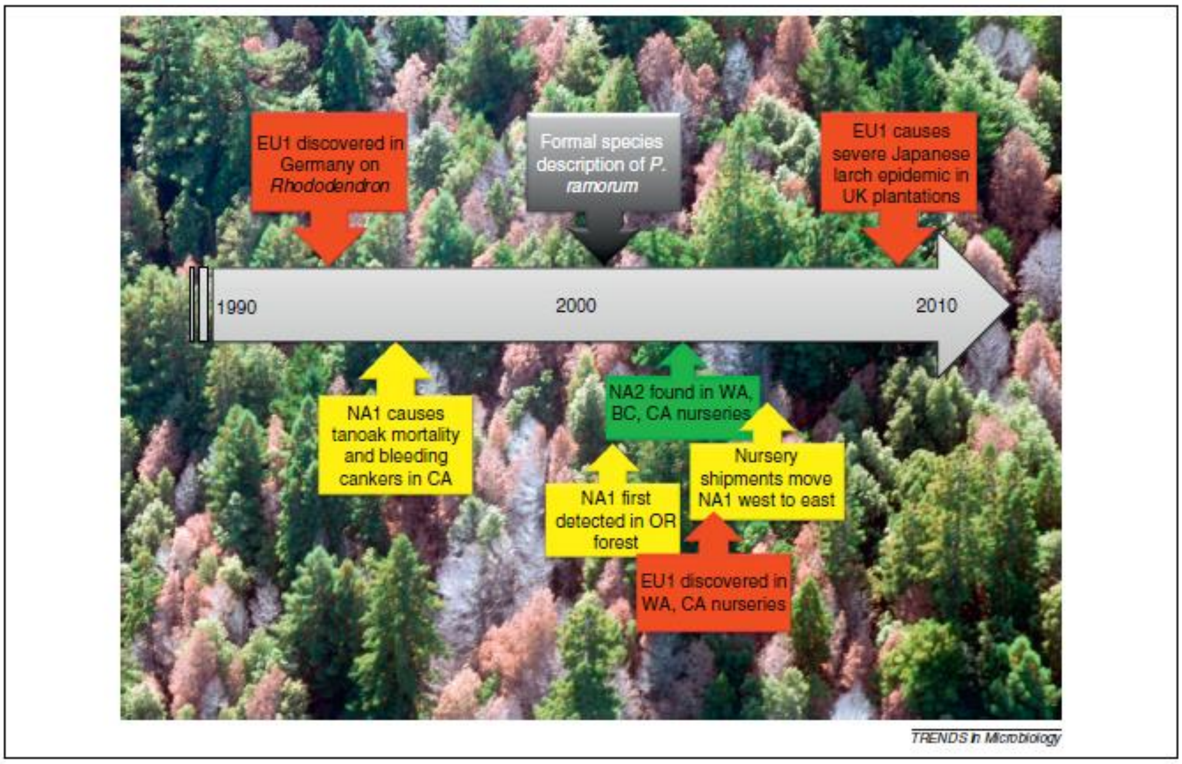


Figure 4: Geographical distribution of *Phytophthora ramorum* according to the EPPO database

2.2 Genetic and phenotypic diversity

The American and European populations have low genetic diversity, consistent with the hypothesis of a "bottleneck" following the introduction of this exotic species on both continents, which was most likely due to the commercial plant trade. *P. ramorum* has two mating types, which have never been observed simultaneously on the same site. The vast majority of European isolates are of the A1 mating type, with the exception of three Belgian A2 isolates (Vercauteren *et al.,* 2010). Conversely, in the United States, isolates are of the A2 mating type.

On each continent, populations are structured into clonal lineages (Mascheretti *et al.*, 2008; Grünwald *et al.*, 2012; Figure 5). The dominant EU1 lineage has been widespread in Europe since 1993, in confined and natural environments. The French isolates all belong to the EU1 lineage. A second EU2 lineage has been found in southern Scotland and Northern Ireland on different plants in natural or forest environments (Van Poucke *et al.,* 2012). The first lineage observed in California in natural environments was named NA1. A second NA2 lineage, of the same A2 mating type, was then observed in nurseries on the west coast (Ivors *et al.*, 2006; Grünwald *et al.*, 2012). Very soon afterwards (2004), the NA1 lineage was found in nurseries on the east coast of the United States, and the EU1 lineage was detected in nurseries, then in forests (Grünwald *et al.*, 2016). The long-standing divergence of the different EU1, EU2, NA1 and NA2 lineages suggests that the American and European populations of *P. ramorum* come from the clonal reproduction of isolated populations, resulting from at least four migration events (Grünwald *et al.*, 2012). *P. ramorum* was recently identified in the mountainous areas of northern Vietnam and it has been suggested that this taxon could be indigenous to this region, which is rich in rhododendron species (Webber *et al.*, 2017).



TRENDS in Microbiology

Figure 5: Approximate chronology of the emergence of *Phytophthora ramorum*, the agent of sudden oak death. The colours indicate the clonal lineages: red = EU1, yellow = NA1 and green = NA2 (Grünwald *et al.*, 2012).

Although clonal and descending from the same individual, the lineages are made up of several multilocus genotypes (MLGs), defined from microsatellite markers. Within the EU1 lineage, one MLG (EU1MG1) is largely dominant in Switzerland, Belgium and Spain (Vercauteren *et al.*, 2010; Perez-

Sierra *et al.*, 2011; Prospero *et al.*, 2013). In the United Kingdom, the *P. ramorum* population is made up of two subpopulations, one sub-population called "European" including EU1MG1 – again dominant – and other MLGs already identified in continental Europe, and another sub-population called "British", consisting of MLGs only found in Great Britain (Harris *et al.,* 2018). The isolates associated with the epidemic observed on larch in the United Kingdom (after 2009) mainly belong to the European subpopulation, while pre-epidemic isolates (obtained from 26 different hosts in the wild) mainly belong to the British subpopulation. Harris *et al.* (2018) suggested that there was two successive introductions of the EU1 lineage in the United Kingdom: the first is the source of the British subpopulation and the second is linked to other European populations and characterised by strong dominance of a common MLG.

The French larch isolates studied have been assigned to the EU1 lineage (Schenck *et al.*, 2018). Of the two isolates analysed by microsatellite, one belongs to the dominant EU1MG1 MLG and the other is a genotype that has not yet been described, related to the dominant European genotype. Both are different from typical genotypes of the British subpopulation (Schenck, personal communication).

The different populations and lineages differ genetically but also by a combination of phenotypic traits (Denman *et al.,* 2005a; Werres and Kaminski, 2005; Brasier *et al*., 2006; Boutet *et al.*, 2009; Manter *et al*., 2010; Vercauteren *et al.*, 2010; Elliott *et al*., 2011; Perez-Sierra *et al*., 2011; Van Poucke *et al.*, 2012; Eyre *et al.*, 2015; Franceschini *et al*., 2014; Harris and Webber, 2016). A recent study (O'Hanlon *et al.,* 2017) compared the four lineages. It reported significant differences between lineages in *in vitro* growth rates at different temperatures (EU2 > NA2 > EU1 > NA1 > NA1) and in aggressiveness (measurements of lesions on detached and wounded rhododendron leaves, NA2 > EU1 > EU2 > NA1). High variability was also observed within lineages regardless of the measured trait. Concerning pathogenicity, no host specificity has been reported in *P. ramorum*. However, Grünwald *et al.* (2008) showed that the original host of the isolates had a significant effect on their aggressiveness. In the same line, within the NA1 lineage, differences in aggressiveness between isolates obtained from hosts with foliar lesions (*Umbellularia californica* and *Notholithocarpus densiflorus*) and isolates obtained from bleeding trunk lesions of *Quercus agrifolia* have been reported (higher aggressiveness of "foliar" isolates than "trunk" isolates, Huberli and Garbelotto, 2012). An epigenetic origin has been proposed for this intra-lineage variation (Kasuga *et al*., 2012). Within the EU1 lineage, isolates from the European subpopulation (associated with larch and the EU1MG1 MLG) were characterised by a higher rate of sporulation on rhododendron and larch leaves than isolates from the British subpopulation (Harris *et al.*, 2018). If these differences observed *in vitro* between the two subpopulations reflect fitness differences, they could explain the high prevalence of the EU1MG1 genotype in the *P. ramorum* population and the emergence of the disease on larch.

2.3 Infection cycle – Identification of different host types

P. ramorum is a generalist pathogen infecting a very broad range of hosts. The epidemic in the wild in California, in an area with a great diversity of species, showed that hosts can be distinguished according to the symptoms expressed (location, type and severity), but also according to their role in the pathogen's epidemiological cycle.

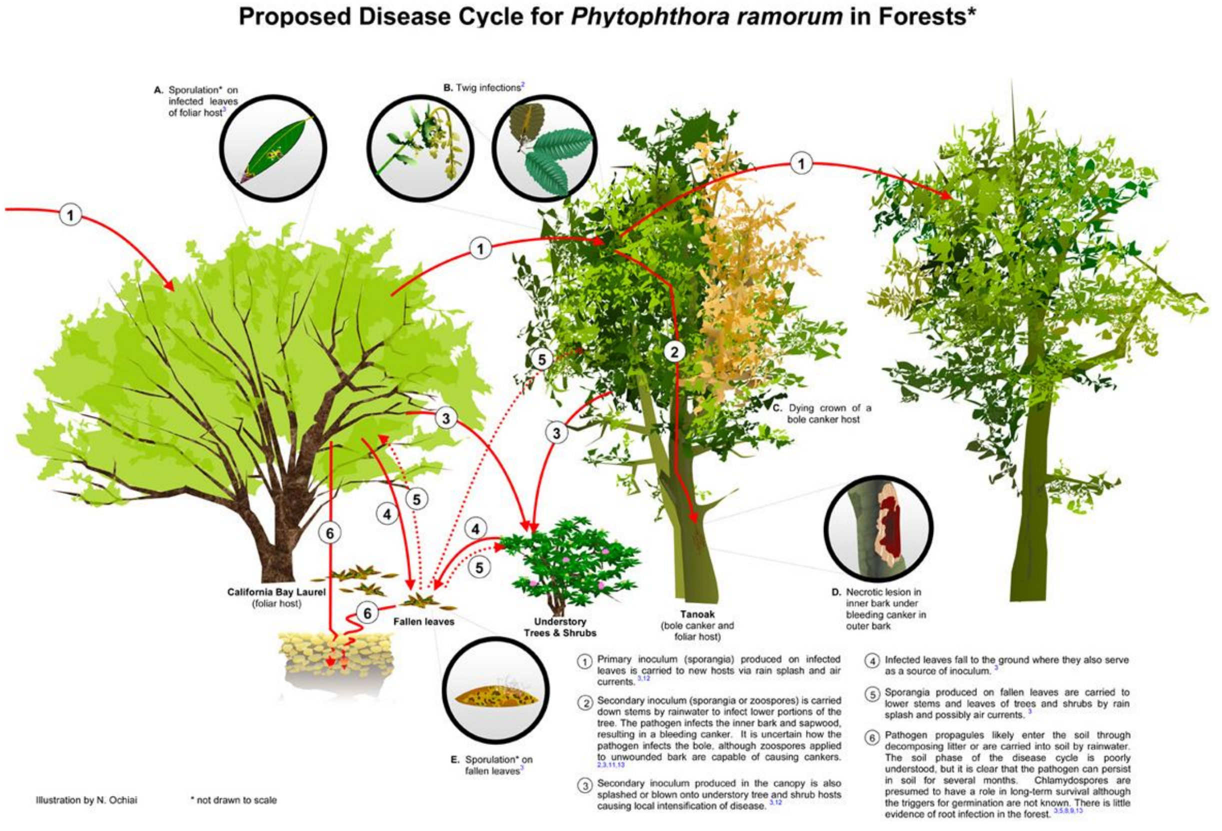
Symptoms may present as leaf necrosis, branch mortality ("blight") or trunk cankers, with a moderate to lethal impact on the plant (Rizzo *et al*., 2005; Figure 6).

Figure 6: Symptoms of sudden oak death (SOD) caused by *Phytophthora ramorum* in California. Top, and bottom left: on coast live oak (*Quercus agrifolia*); bottom centre: on tanoak (*Notholithocarpus densiflorus*); bottom right: on *Azalea* or *Rhododendron* leaves (from Rizzo *et al*. 2005).

Symptom type and damage severity are not completely independent: leaf infections by themselves, when not extended to stems and branches, are generally not lethal to the host (e.g. on California bay laurel *Umbellularia californica*), unlike trunk cankers, which may be associated with mortality (Davidson *et al.*, 2005; Anacker *et al*., 2008; Liu *et al*., 2007). In addition, there may be variations in severity for a given symptom type between species, for example in tanoak (*Notholithocarpus densiflorus*), which is much more susceptible than oak (Grünwald *et al*., 2008), or between individuals of a species, as shown for example with *Q. agrifolia* (Conrad *et al*., 2017).

Phytophthora ramorum has the relatively rare characteristic among *Phytophthora* species affecting temperate forest trees (and never observed before the sudden oak death epidemic in California) of being able to disperse by air, via its sporangia (asexual reproductive organs containing zoospores). In the case of sudden oak death, it has been shown that this airborne transmission has played a decisive role in the epidemic progression of the disease in California (Davidson *et al*., 2005 and 2008).

An unexpected observation from studies on sudden oak death carried out in the United States was that *P. ramorum* is able to sporulate only on certain hosts, and that conversely, some otherwise highly susceptible hosts such as *Quercus agrifolia,* which are only infected on their trunks, do not seem to allow production of sporangia (and therefore transmission/dissemination of the oomycete). All tests designed to identify sporangia in cortical tissue of *Q. agrifolia* or in exudates have been negative, while many sporangia have been found on infected leaves of California bay laurel (*Umbellularia californica*) (Davidson *et al*., 2005 and 2008). As a result of these observations, a relatively complex infection cycle with different host types has been proposed (Figure 7, Parke and Lucas, 2008).



① Primary inoculum (sporangia) produced on infected leaves is carried to new hosts via rain splash and air currents. [3,12]

② Secondary inoculum (sporangia or zoospores) is carried down stems by rainwater to infect lower portions of the tree. The pathogen infects the inner bark and sapwood, resulting in a bleeding canker. It is uncertain how the pathogen infects the bole, although zoospores applied to unwounded bark are capable of causing cankers. [2,3,11,13]

③ Secondary inoculum produced in the canopy is also splashed or blown onto understory tree and shrub hosts causing local intensification of disease. [3,12]

④ Infected leaves fall to the ground where they also serve as a source of inoculum. [3]

⑤ Sporangia produced on fallen leaves are carried to lower stems and leaves of trees and shrubs by rain splash and possibly air currents. [3]

⑥ Pathogen propagules likely enter the soil through decomposing litter or are carried into soil by rainwater. The soil phase of the disease cycle is poorly understood, but it is clear that the pathogen can persist in soil for several months. Chlamydospores are presumed to have a role in long-term survival although the triggers for germination are not known. There is little evidence of root infection in the forest. [3,5,8,9,13]

Figure 7: Life cycle of *Phytophthora ramorum* (Source: Parke and Lucas, 2008; see full legend on:
https://www.apsnet.org/edcenter/disandpath/oomycete/pdlessons/Pages/SuddenOakDeath.aspx

Some hosts such as California bay laurel (*U. californica*), with foliar infections and producing secondary inoculum (sporangia), are described as sporulating, infectious (Hüberli and Garbelotto, 2012) or transmissive (Garbelotto *et al*., 2017) foliar hosts (Figure 7, left). Conversely, other species such as *Quercus agrifolia*, with bleeding cortical cankers on their trunks (and no foliar symptoms), have no spore production and do not participate in transmission of the epidemic (Davidson *et al*., 2005). They are then referred to as "dead-end" hosts (Davidson *et al*., 2005; Grünwald *et al*., 2008; Hüberli and Garbelotto, 2012; Garbelotto *et al*., 2017) or sometimes as "terminal hosts" (Liu *et al*., 2007; Brown and Allen-Diaz, 2009; McPherson *et al*., 2010; Conrad *et al*., 2017). Lastly, some species such as tanoak (*Notholithocarpus* or *Lithocarpus densiflorus*, in the centre of the figure above) may have both types of symptoms and therefore produce secondary inoculum on leaves and develop trunk cankers (Grünwald *et al*., 2008).

2.4 Natural dispersal

The modes of dispersal of *P. ramorum* have been fairly well characterised by work carried out in the United States and Great Britain. *P. ramorum* is mainly spread by aerial dispersal, with dissemination of wind-blown water droplets generated by splashing (Rizzo *et al*., 2005). This was established by characterising the spatial pattern of infection on susceptible hosts caused by inoculum from a known infected source.

This spread is generally short-range, with about 50% of infections within 120 m and 80% within 300 m (Hansen *et al.*, 2008; Webber *et al.*, 2010), but with a small proportion of dispersal events at greater distances (up to 2-4 km, Hansen *et al.*, 2008; Peterson *et al.*, 2015). These long-distance dispersal events may result from splashing during gusts of wind, or may be the consequence of other modes of dispersal (see below). Trapping of *P. ramorum* spores (rainwater harvesting traps with leaf baiting) has been documented 250 m away from inoculum sources (Webber *et al*., 2010), which is consistent with the range of dispersal distances reported. The maximum observed dispersal distance depends on the years and, in particular, on the climate (spring rainfall in year n-2) and the size of the contaminated area; it increases with the size of the outbreak and therefore with time (Peterson *et al*., 2015). This is in line with the theory of epidemic spread, which states that the velocity of spread of many diseases accelerates over time (Scherm, 1996). Another characteristic is that the dispersal distance increases with the height of the inoculum source: about 100 m from a tree (larch, *Notholithocarpus*), but only about 10 m from a shrub (rhododendron) according to British experience (Brasier *et al.*, 2006).

Survival of the inoculum (chlamydospores and sporangia) in soil (Davidson *et al*., 2005; Cushman and Meentemeyer, 2008; Eyre *et al*., 2013) and water (Sutton *et al*., 2009; Davidson *et al*., 2005; Eyre and Garbelotto, 2015) could contribute to the dispersal of *P. ramorum.* The contribution of these dispersal modes appears to be very low compared to air dispersal under natural conditions (Eyre *et al*., 2013; Peterson *et al*., 2014a). In Oregon, the distribution of *P. ramorum* outbreaks in relation to watercourses did not suggest any effective dispersal of *P. ramorum* by this route (Peterson *et al*., 2014b). However, *P. ramorum* has been found in watercourses with outbreaks upstream (Davidson *et al*., 2005; Sutton *et al*., 2009; Ireland *et al*., 2013; Croucher *et al*., 2013) and under certain conditions, after flooding and waterlogging, *P. ramorum* can infect the foliage of susceptible vegetation on the bank (Chastagner *et al*., 2010). The ability of *P. ramorum* to cause infections from soil has also been demonstrated. Infection can occur from soil to litter, then from infected litter to the lower leaves of susceptible plants (rhododendron in Europe, e.g. in quarantined sites where larch trees have been felled down or *Umbellularia californica* in the US), probably via splashing (Davidson *et al*., 2005; Harris, 2015). *P. ramorum* has a strong ability to persist in the environment. It has been shown to survive for at least two years in infected larch litter after eradication (Harris, 2015). Its ability to infect a wide range of hosts, sometimes at low infection levels and including roots (Fichtner *et al*., 2011), increases its ability to persist in the environment.

The long-distance dispersal of *Phytophthora* species in general, and *P. ramorum* in particular, mainly occurs due to human activities (see §5 below). Dispersal by movement of contaminated plants is well established and is the main vector for movement between continents or countries (Goss *et al*., 2009; Jung *et al*., 2016; Migliorini *et al*., 2015).

3 Classification of species according to their susceptibility to *Phytophthora ramorum*

3.1 Definitions and terminology used in this report

As shown by the observations in California, the concept of susceptibility to *P. ramorum* encompasses different aspects. The existence of "dead-end" hosts (not allowing spore-formation and therefore not involved in epidemic development) has rarely been observed in plant pathology with the exception of a few reports regarding phytoplasmas (Alma *et al*., 2000) or viruses (Morilla *et al*., 2005). The term "**terminal host**" used to describe these hosts, which has not yet been used in plant pathology, may be ambiguous. This term is sometimes used in animal parasitology in the same meaning as "dead-end" host, but classically, the notion of terminal or definitive host refers to the development stages of heteroxenic parasites (i.e. requiring several successive hosts to complete their life cycle, which is not the case for *P. ramorum*): in this case, the "final", "terminal" or "definitive" hosts are those in which the parasite reaches maturity and performs sexual reproduction (Odening, 1976; Mehlhorn, 2008).

It therefore seemed important to us to clarify the concept of susceptibility, by distinguishing on the one hand the ability of a species to develop symptoms and damage as a result of infection, and on the other hand, its ability to multiply and transmit the pathogen after being infected, thus necessarily to allow its sporulation (see Figure 8). For the first component, we will use the term **vulnerability**. For the second component, we will use **competence** (Johnson *et al*., 2013). The concept of host competence has often been used in recent literature when dealing of disease transmission within more or less diverse communities, particularly in relation to the hypothesis of a dilution effect, i.e. a reduction in disease risk associated with an increase in the diversity of communities (the opposite would be an amplification effect). This effect may be explained by differences in competence (i.e. ability to transmit) between species for the pathogen involved. A dilution effect was observed for *P. ramorum* in a study in southern California (Haas *et al*., 2011).

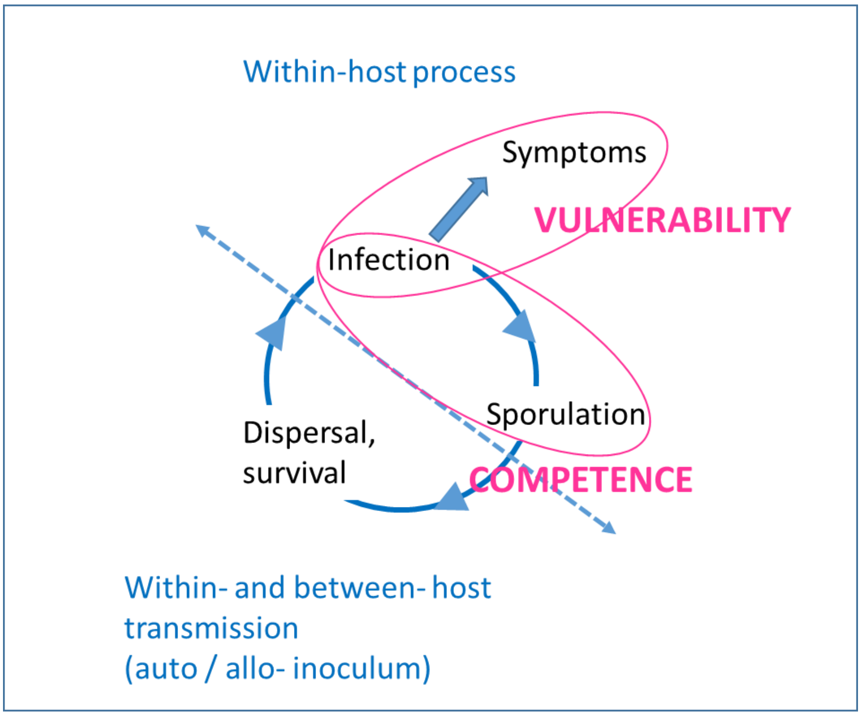


Figure 8: Conceptual scheme of the various components of a plant's susceptibility to a pathogen, for example to *Phytophthora ramorum*

Vulnerability and competence are not necessarily correlated. As seen above, highly competent species may have few symptoms and therefore low vulnerability (as in the case of California bay laurel), or vice versa (as in the case of *Quercus agrifolia*, with mortality but no sporulation). However, **competence interacts with vulnerability to characterise the risk associated with *P. ramorum* for a given species**. Indeed, for equivalent vulnerability, a tree of a competent species, which therefore multiplies the pathogen, will potentially be exposed to a larger inoculum (auto- and allo-inoculum), and will therefore be more infected and undergo more damage, than a tree of a non-competent species (*Notholithocarpus densiflorus* and *Larix kaempferi* are examples of species that are both vulnerable and competent).

Competence characterises not only the susceptibility of a given species but also the epidemic risk associated with this species towards other tree species in its vicinity, due to inoculum transmission.

3.2 List of plant species considered

Given the context and the issues at stake, particular care was taken to summarise the information available on the susceptibility of ***Larix* species.**

We then considered several lists of plants whose susceptibility needed to be characterised:

- forest tree species regulated by the French Forestry Code updated in July 2017, i.e. 66 species (Ministry of Agriculture website: http://agriculture.gouv.fr/fournisseurs-especes-reglementees-provenances-et-materiels-de-base-forestiers);

- the other forest tree species found in France; the list was compiled from data of the National Forest Inventory (IFN) from 2005 to 2016 (https://inventaire-forestier.ign.fr/), comprising a total of 119 tree species (defined here by height >8 m, excluding vines). All tree species not previously taken into account were selected, i.e. 70, giving a total of 136 regulated or unregulated species of trees;

- accompanying forest species, also defined from IFN data. Of the 201 shrub species (woody species <8 m) found among the nearly 860,000 observed plots, we selected species found in more than 5% plots in at least one of the major regions (North-West, South-West, North-East, South-West), i.e. 47;

- tree and shrub species not generally found in forests in France (not previously taken into consideration), but sometimes found in other European countries or potentially in parks and gardens, often exotic ornamental species, previously identified as hosts of *P. ramorum*.

3.3 Search and data synthesis on species susceptibility

In order to supplement the experts' documentary resources, the Scopus and WoS databases were queried by cross-referencing "*Phytophthora ramorum*" with "susceptibility" or "resistance" or "host range". More specifically, each genus name on the forest species lists (most frequent trees and accompanying species) was cross-referenced with *P. ramorum* in WoS and each species name in Google Scholar. Primary articles in international peer-reviewed journals, as well as reviews, other publications and conference proceedings were all examined. In total, our database contained 135 references. In practice, a much smaller number of them contained information relevant to answering the question of the susceptibility of European species (see below).

We also compiled lists/reviews on the susceptibility of species, particularly European species, that had already been drawn up by several other organisations:

- EPPO global database: list of hosts and reports under natural conditions ("Reporting");

- UK Ministry of Agriculture (DEFRA): FERA list of natural hosts for *Phytophthora ramorum* with symptom and location (https://planthealthportal.defra.gov.uk/assets/uploads/P-ramorum-host-list-finalupdate-NOV-20-15.pdf);

- European RAPRA project (http://rapra.csl.gov.uk), especially Appendices II (natural hosts) and III (species susceptibility under environmental conditions) of the deliverable on risk assessment (Sansford *et al.,* 2009);

- Forestry Commission (https://www.forestry.gov.uk/pramorum): in particular, advice on the choice of reforestation species in contaminated areas (Webber 2010, revision 2017 https://www.forestry.gov.uk/pdf/FCReplantingRecommendationsRevised2017.pdf/$FILE/FCReplantingRecommendationsRevised2017.pdf);

- Ireland:

https://www.agriculture.gov.ie/media/migration/farmingsectors/planthealthandtrade/2PPINPhytophthoraRamorumFeb2012.pdf

- CABI: https://www.cabi.org/isc/datasheet/40991;
- APHIS: https://www.aphis.usda.gov/plant_health/plant_pest_info/pram/downloads/pdf_files/usdaprlist.pdf;
- Canada: http://www.inspection.gc.ca/plants/plant-pests-invasive-species/directives/horticulture/d-01-01/appendix-1/eng/1363039571899/1363039666772.

3.4 Classification methodology – typology of species for susceptibility to *Phytophthora ramorum*

We sought to apply the methodology proposed by the ANSES MRA WG (2016), with the establishment of lines of evidence, integration of the lines of evidence and expression of the weight of evidence, regarding species susceptibility. The lines of evidence here concern the results of different studies corresponding to the same susceptibility criterion, such as the frequency of infection under natural conditions, or sporulation under controlled conditions.

From the data collected, we selected five susceptibility criteria (variables), characterised according to the bibliography:

(1) symptom type (affected organ) under natural conditions: no symptoms/ leaf blight/ shoot dieback/ cortical cankers (same terminology as adopted in the FERA list (2015));

(2) frequency of symptoms under natural conditions;

(3) severity of symptoms on cortical tissues (trunks and stems) after controlled inoculations;

(4) severity of leaf symptoms after controlled inoculations;

(5) ability to produce secondary inoculum (chlamydospores and especially sporangia).

The WG experts first extracted the information from each publication and then sought to code it into categories for the five criteria. For each criterion, the WG considered two, three or four categories. For example, for natural infections: existence/absence of reports (two categories), no reports/rare reports/moderate to very frequent reports (three categories), no reports/rare reports/moderately frequent reports/numerous reports (four categories). An independent cross-validation study was carried out by three experts for 16 species and nine references (those containing the largest number of compared species). Given the relative paucity of information (see below), we did not think it reasonable to have a higher number of categories (Table 1).

Table 1: Summary and coding of literature data on species susceptibility to *P. ramorum*

Susceptibility variable	Categories	Explanation
Frequency of natural infections	0 1 2	Never mentioned Rare (estimated to be fewer than 10 independent reports = different sites) Occasional to frequent
Type of natural symptoms	F D C	Foliar (leaf blight) shoot Dieback cortical Cankers on trunks
Susceptibility of stem and trunk cortical tissue (controlled inoculation with wound)	Nd 1 2	No data Not susceptible/Low susceptibility Moderately to highly susceptible
Leaf susceptibility after controlled inoculation (without wound)	Nd 1 2	No data Not susceptible/Low susceptibility Moderately to highly susceptible
Sporulation on leaves*	Nd 1 2	No data Sporulation not significant Sporulation significant

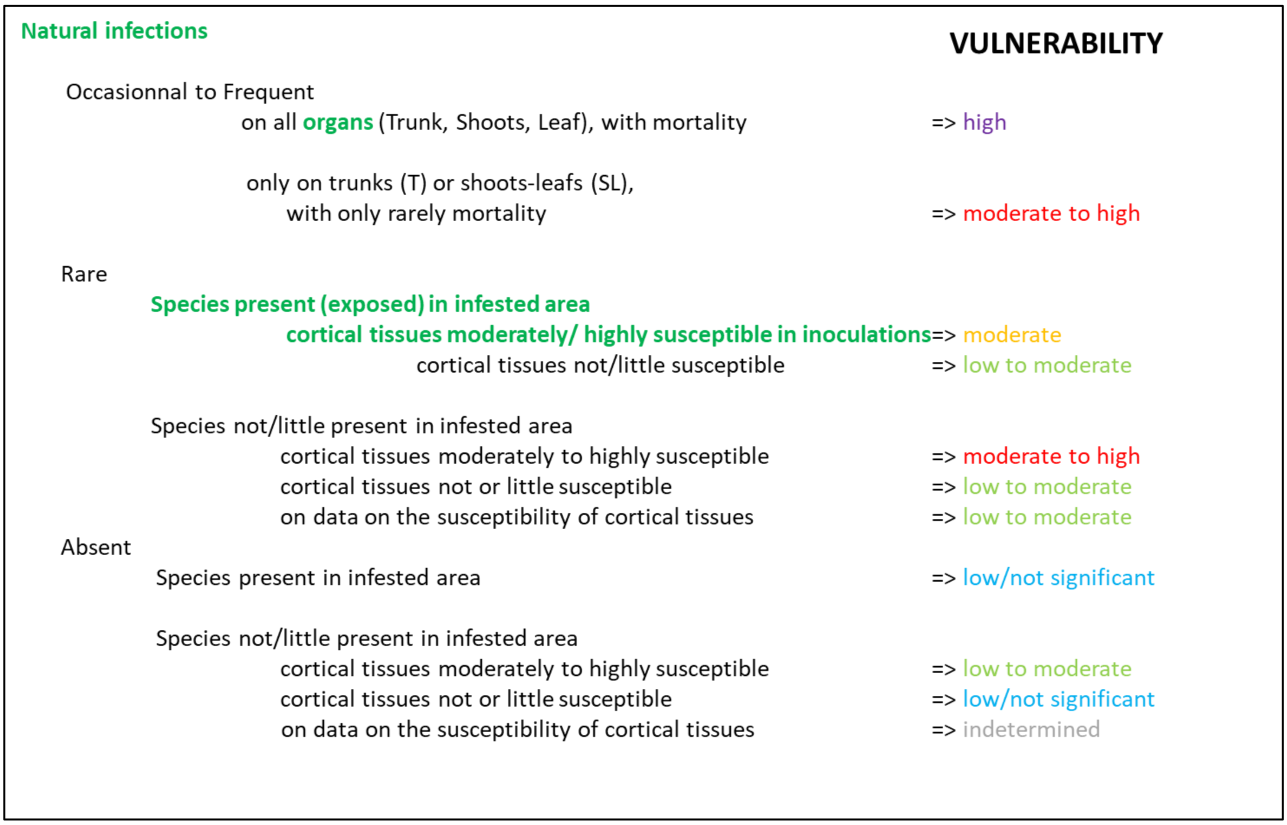
* Generally under controlled conditions but some data under natural conditions

As far as possible, thresholds were defined for deciding between one category or another, for example 10 independent reports for the frequency of natural infections, or more than 100 sporangia/cm^2 for *in vitro* sporulation data.

Decision trees taking the five criteria into account (prioritised and used in a reasoned way and not according to a statistical method) were then used to estimate vulnerability and competence (Figures 9 and 10), with a scale of five categories: low, low to moderate, moderate, moderate to high, or high. Uncertainties were estimated as low, moderate, or high, depending on the quantity and consistency of available data. A "not determined" category refers to species for which no data were available.

The assessment of the vulnerability and competence of each species was based heavily on observations under natural conditions, which correspond to a proven risk of developing symptoms and/or promoting epidemic development. For species with low infection under natural conditions, we considered whether or not they were exposed to natural inoculum, before taking artificial inoculation data into account. Exposure was estimated by considering the abundance of the species in the area affected by the disease in California and Oregon, and especially in western Great Britain (which shares more species with France). The distribution data for Great Britain were taken from https://bsbi.org/. We took *Larix kaempferi* and *L. decidua* as references, which are reported in almost all quadrats with longitude <-3°, while species regarded as "not exposed or not very exposed" were those with a more limited distribution (absent from part of the quadrats with longitude <-3°).

The assessment of vulnerability took into account the frequency and severity of natural infections supplemented by the results of inoculations under controlled conditions, mainly considering symptoms on branches and trunks, which are more likely to induce mortality compared to symptoms limited to leaves. In most cases, naturally infected species also have high susceptibility under artificial inoculation conditions. However, Harris' work in particular (2015) showed great variation in susceptibility variables for the same species after artificial inoculation (symptom expression, re-isolation), which could be related to the isolates or the time of year (peak susceptibility in spring), as well as between trees or even between needles from the same shoot, which could in some cases explain differences between studies. When several studies yielded different results, we considered the highest susceptibility values.



Natural infections

VULNERABILITY

Occasionnal to Frequent
on all **organs** (Trunk, Shoots, Leaf), with mortality => high

only on trunks (T) or shoots-leafs (SL),
with only rarely mortality => moderate to high

Rare
Species present (exposed) in infested area
cortical tissues moderately/ highly susceptible in inoculations=> moderate
cortical tissues not/little susceptible => low to moderate

Species not/little present in infested area
cortical tissues moderately to highly susceptible => moderate to high
cortical tissues not or little susceptible => low to moderate
on data on the susceptibility of cortical tissues => low to moderate

Absent
Species present in infested area => low/not significant

Species not/little present in infested area
cortical tissues moderately to highly susceptible => low to moderate
cortical tissues not or little susceptible => low/not significant
on data on the susceptibility of cortical tissues => indetermined

Figure 9: Decision tree for determining vulnerability categories for forest tree species based on knowledge from the literature (C = Canker, D = dieback, F = Foliar)

The assessment of competence first took into account the observation of self-sustaining epidemics in the wild, i.e. not dependent on the presence of sporulating hosts of another species. Two levels of epidemic development were distinguished, based on the temporal and spatial extent of outbreaks. In the absence of epidemic development, we considered exposure, then the existence of foliar infections under natural conditions, and lastly leaf sporulation data, generally obtained after controlled inoculations. Non-significant sporulation corresponds to a low density of sporangia (<100/cm^2 of leaf), or a confirmed absence of transmission under natural conditions. As with vulnerability, the estimated *in vitro* sporulation rate was highly variable, even between leaves of the same plant, and depended on the age of the leaves (Harris and Webber, 2016). In the event of divergent data, we took the maximum value. The foliar infection criterion was used to characterise competence because only foliar hosts can support *P. ramorum* sporulation, although this is not systematic. However, there is no correlation between sporulation and foliar symptoms after artificial inoculation: high sporulation can be observed on leaves with few necroses or even asymptomatic leaves (DEFRA, 2005; Moralejo, 2006; Harris, 2015).

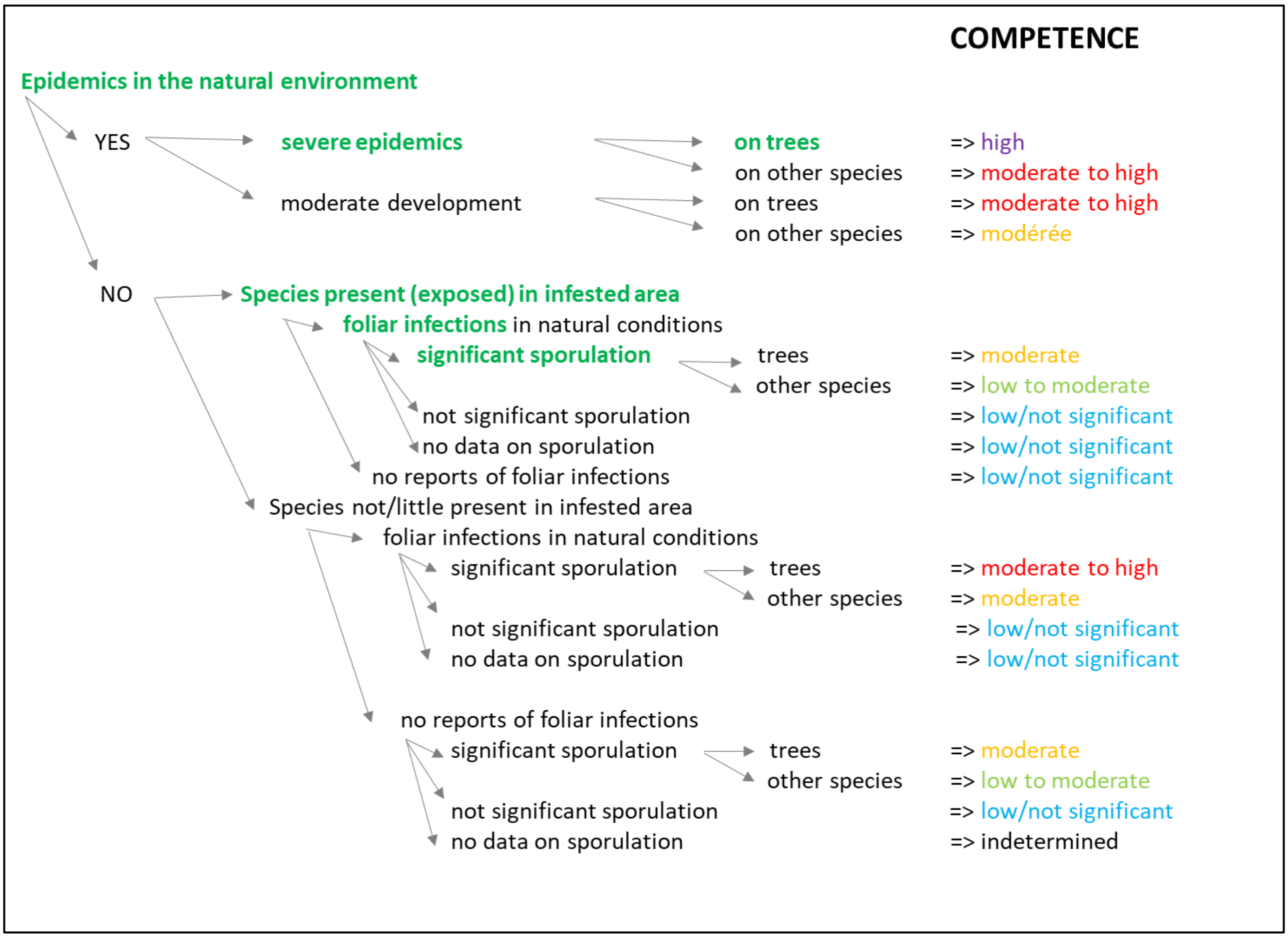


Figure 10: Decision tree for determining competence categories for forest tree species based on knowledge from the literature

For accompanying forest species (shrubs), we only considered their competence (potential role in facilitating epidemics via *Phytophthora* sporulation), estimated in the same way as explained above. However, we differentiated the level of competence according to the height of the species. Hence, the competence of a shrub was regarded as lower than that of a tree with an equivalent sporulation density, due to a shorter expected transmission distance.

For other species not found in French forests, mainly ornamental species, we simply listed all the host species, i.e. all those naturally infected and from which *P. ramorum* had been isolated.

3.5 Results on species susceptibility

3.5.1 Uncertainties

It seems important for us to begin by mentioning that most of the results indicated are subject to moderate to high uncertainties. Indeed, data from the literature are relatively limited for estimating the susceptibility of the multiple potential host species of *P. ramorum*. In Europe, because natural infections in forest stands have only been reported in Great Britain and Ireland, information is only available for species that are well established in these areas. But even for these species, there are few summary data on the frequency (and severity) of natural infections. We mainly relied on EPPO data, the list of natural hosts established by FERA (2015) and the article by King *et al.* (2015) with a list of isolates by host species. The results of studies on the susceptibility of species obtained under controlled conditions, as with any pathogen, should be viewed with caution. For example, foliar infections with (very low) sporulation have been obtained on *Q. agrifolia,* despite it being regarded as an example of a strictly trunk host (Vettraino *et al.*, 2008). In addition, published studies rarely test a large number of species at the same time with susceptible and resistant controls. Few studies are generally available for a given species. In total, fewer than 30 references could be used in addition to the information provided in Sansford *et al.* (2009), 50% of which came from a single team at the Forestry Commission (Joan Webber). Many of the results obtained by J. Webber's team are only available in reports or have so far only been the subject of communications (e.g. Webber *et al.,* 2017, PPT file made available).

3.5.2 Trees

Tables 2 and 3 present summary literature data for the 66 regulated and 70 unregulated tree species.

The classification of species for vulnerability and competence, derived from these data, is shown in Tables 4 and 5 and summarised in Figure 11.

Apart from the three species of larch (*Larix kaempferi, Larix x eurolepis, Larix decidua*) deemed to be highly vulnerable and competent, 10 other species among the regulated species have moderate to high vulnerability and/or competence (see details below). Sweet chestnut (*Castanea sativa*) and three species of oaks (*Quercus ilex, Quercus cerris, Quercus rubra*) have at least moderate vulnerability and competence. Beech (*Fagus sylvatica*), grand fir (*Abies grandis*), Douglas fir (*Pseudotsuga menziesii*) and Sitka spruce (*Picea sitchensis*) have at least moderate vulnerability, but no significant competence. Conversely, ash (*Fraxinus excelsior*) and black locust or false acacia (*Robinia pseudoacacia*) have moderate competence but low (or not determined) vulnerability.

Among the unregulated tree species, those with moderate to high vulnerability are *Abies procera, Arbutus unedo, Chamaecyparis lawsoniana, Quercus falcata, Taxus baccata* and *Tsuga heterophylla*. The species with moderate to high competence are *Aesculus hippocastanum, Arbutus unedo, Eucalyptus viminalis* and *Ulmus procera.*

Table 2: Summary data from the literature on the susceptibility to *Phytophthora ramorum* of regulated forest tree species in France

Latin name	**Common name**	**Natural infection frequency**	**Exposure**	**Symptoms of natural infection**	**Trunk suscep-tibility**	**Leaf suscep-tibility**	**Sporulation**	**References**
Abies alba Mill.	European silver fir	1	1	B	nd	nd	nd	Sansford *et al.*, 2009, FERA 2015
Abies bornmuelleriana Mattf.C	Turkish fir	0	1		nd	nd	nd	
Abies cephalonica Loud.	Greek fir	0	1		nd	nd	nd	
Abies grandis Lindl.	Grand fir	1	1	FBT	2	2	1	Sansford *et al.*, 2009, FERA 2015, King *et al.*, 2015
Abies pinsapo Boiss.	Spanish fir	0	1		nd	nd	nd	
Acer campestre L.	Field maple	0	2		2	1	nd	Sansford *et al.*, 2009,
Acer platanoides L.	Norway maple	0	1		2	1	nd	Sansford *et al.*, 2009
Acer pseudoplatanus L.	Sycamore	1	2	T	1	2	1	Sansford *et al.*, 2009, FERA 2015, King *et al.*, 2015, DEFRA 2004
Alnus cordata (Loisel.) Duby.	Italian alder	0	1		nd	nd	nd	
Alnus glutinosa Gaertn.	European alder, black alder	0	2		1	2	nd	Sansford *et al.*, 2009, Rytkönen *et al.*, 2012
Alnus incana Moench.	Grey alder	0	1		1	nd	nd	Sansford *et al.*, 2009,
Betula pendula Roth	Silver birch	1	2	T	1	1	nd	Sansford *et al.*, 2009, FERA 2015, King *et al.* 2015, Rytkönen *et al.* 2012
Betula pubescens Ehrh.	White birch	1	2	?	1	nd	nd	Sansford *et al.*, 2009, EFSA 2011
Carpinus betulus L.	Hornbeam	0	2		1	2	nd	Sansford *et al.*, 2009,
Castanea sativa Mill.	Sweet chestnut	2	2	FBT	1	2	2	Sansford *et al.*, 2009, FERA 2015, King *et al.* 2015, Harris & Webber 2006
Cedrus atlantica Carr.	Atlas cedar	0	1		nd	nd	nd	
Cedrus libani A. Richard	Cedar of Lebanon	0	1		nd	nd	nd	
Eucalyptus globulus Labill.	Tasmanian blue gum	0	1		nd	nd	nd	Sansford *et al.*, 2009,
Eucalyptus gunnii x dalrympleana	Eucalyptus gundal	0	1		nd	nd	nd	Sansford *et al.*, 2009,
Fagus sylvatica L.	Beech	2	2	FT	2	1	1	Sansford *et al.*, 2009, FERA 2015, King *et al.*, 2015
Fraxinus angustifolia Vahl.	Narrow-leaved ash	0	1		1	2	nd	Sansford *et al.*, 2009, Moralejo *et al.*, 2009
Fraxinus excelsior L.	Common ash	1	2	F	1	2	2	Sansford *et al.*, 2009, FERA 2015, King *et al.*, 2015
Juglans major x regia L.	Hybrid walnut	0	1		nd	nd	nd	
Juglans nigra L.	Black walnut	0	1		2	nd	nd	Sansford *et al.*, 2009
Juglans nigra x regia L.	Hybrid walnut	0	1		nd	nd	nd	

Juglans regia L.	English walnut, common walnut	0	1		nd	nd	nd	
Larix decidua Mill.	European larch	2	2	FBT	2	2	2	FERA 2015, King *et al.*, 2015, Harris & Webber 2016
Larix x eurolepis Henry	Hybrid larch	2	2	FBT	2	2	2	FERA 2015, Harris & Webber 2016
Larix kaempferi Carr.	Japanese larch	2	2	FBT	2	2	2	FERA 2015, Harris & Webber 2016
Larix sibirica Ledeb.	Siberian larch	0	1		nd	nd	nd	
Malus sylvestris Mill.	Crab apple	0	2		nd	1	nd	Sansford *et al.*, 2009,
Picea abies Karst.	Norway spruce	0	2		1	2	nd	Sansford *et al.*, 2009, Rytkönen *et al.*, 2012
Picea sitchensis Carr.	Sitka spruce	1	2	B	2	2	nd	Sansford *et al.*, 2009, FERA 2015
Pinus brutia Ten.	Turkish pine	0	1		nd	nd	nd	
Pinus canariensis C.Smith	Canary Island pine	0	1		nd	nd	nd	
Pinus cembra L.	Swiss stone pine	0	1		nd	nd	nd	
Pinus contorta Loud.	Lodgepole pine	0	1		1	1	nd	Sansford *et al.*, 2009
Pinus halepensis Mill.	Aleppo pine	0	1		2	nd	nd	Sansford *et al.*, 2009, Moralejo *et al.*, 2009
Pinus leucodermis Antoine	Bosnian pine	0	1		nd	nd	nd	
Pinus nigra Arn. (and sub-species)	Black pine	0	1		1	1	nd	Sansford *et al.*, 2009, Moralejo *et al.*, 2009
Pinus pinaster Aït	Maritime pine	0	1		1	nd	nd	Sansford *et al.*, 2009, Moralejo *et al.*, 2009
Pinus pinea L.	Stone pine, parasol pine	0	1		2	nd	nd	Sansford *et al.*, 2009, Moralejo *et al.*, 2009
Pinus radiata D. Don	Monterey pine	0	1		2	1	nd	Sansford *et al.*, 2009, Hüberli *et al.*, 2008
Pinus sylvestris L.	Scots pine	0	2		1	1	nd	Sansford *et al.*, 2009, Moralejo *et al.*, 2009, Rytkönen *et al.*, 2012
Pinus taeda L.	Loblolly pine	0	1		nd	nd	nd	
Populus nigra L.	Black poplar	0	1		nd	nd	nd	
Populus trichocarpa L.	Black cottonwood	0	1		1	1	nd	Sansford *et al.*, 2009
Populus ssp.	Hybrid cultivars	0	1		1	nd	nd	Sansford *et al.*, 2009
Populus tremula L.	Aspen	0	2		nd	2	nd	Sansford *et al.*, 2009
Prunus avium L.	Sweet cherry, wild cherry	0	2		nd	2	nd	Sansford *et al.*, 2009
Pseudotsuga menziesii (Mirb.) Franco	Douglas fir	2	2	FBT	2	2	1	Sansford *et al.*, 2009, Ramage *et al.*, 2012, FERA 2015, Forrestel *et al.*, 2015, King *et al.* 2015
Quercus cerris L.	Turkey oak	2	2	FT	2	2	2	Sansford *et al.*, 2009, FERA 2015, King *et al.*, 2015

Quercus ilex L.	Holm oak	2	1	FB	2	2	2	Sansford *et al.*, 2009, Denman *et al.*, 2009, Moralejo *et al.*, 2009, FERA 2015, King *et al.*, 2015
Quercus petraea Liebl.	Sessile oak	1	2	T	1	2	2	Sansford *et al.*, 2009, FERA 2015, King *et al.*, 2015
Quercus pubescens Willd.	Downy oak	0	1		2	nd	nd	Sansford *et al.*, 2009, Moralejo *et al.*, 2009
Quercus robur L.	English oak, pedunculate oak	1	2	T	1	1	2	Sansford *et al.*, 2009, Rytkönen *et al.*, 2012, FERA 2015
Quercus rubra L.	Northern red oak	1	1	T	2	1	2	Sansford *et al.*, 2009, Jinek *et al.*, 2011, Tooley *et al.*, 2011, FERA 2015, King *et al.*, 2015
Quercus suber L.	Cork oak	0	1		2	1	nd	Sansford *et al.*, 2009, Moralejo *et al.*, 2009
Robinia pseudoacacia L.	False acacia, black locust	0	1		nd	2	2	Sansford *et al.*, 2009, Tooley *et al.*, 2009, Bulajic *et al.*, 2010, EFSA 2011
Sorbus domestica L.	Service tree	0	1		nd	nd	nd	
Sorbus torminalis L.	Wild service tree	0	1		nd	nd	nd	
Tilia cordata Mill.	Small-leaved lime, small-leaved linden	0	1		1	2	nd	Sansford *et al.*, 2009
Tilia platyphyllos Scop	Large-leaved lime, large-leaved linden	0	1		nd	nd	nd	Sansford *et al.*, 2009

Table 3: Summary data from the literature on the susceptibility to *Phytophthora ramorum* of unregulated forest tree species in France

Latin name	**Frequency of natural infection**	**Exposure**	**Symptoms of natural infection**	**Trunk susceptibility**	**Leaf susceptibility**	**Sporulation**	**References**
Abies nordmanniana	0	1		nd	nd	nd	
Abies procera	1	1	BT	2	2	nd	Sansford *et al.*, 2009
Acer monspessulanum	0	1		1	1	nd	Sansford *et al.*, 2009, Moralejo *et al.*, 2009
Acer negundo	0	1		nd	nd	nd	
Acer opalus subsp. opalus	0	1		nd	nd	nd	
Aesculus hippocastanum	1	2	FT	1	2	2	Sansford *et al.*, 2009
Ailanthus altissima	0	1		nd	nd	nd	
Arbutus unedo	1	1	FB	2	2	2	Sansford *et al.*, 2009
Cedrus deodara	0	1		nd	nd	nd	
Celtis australis	0	1		1	2	nd	Sansford *et al.*, 2009, Moralejo *et al.*, 2009
Cercis siliquastrum	0	1		1	2	nd	Sansford *et al.*, 2009
Chamaecyparis lawsoniana	1	1	BT	2	1	nd	Sansford *et al.*, 2009
Corylus avellana	0	1		1	2	nd	Sansford *et al.*, 2009

Crataegus laevigata	0	1		nd	nd	nd	
Crataegus monogyna	0	1		1	1	1	Sansford *et al.*, 2009
Cryptomeria japonica	0	1		nd	nd	nd	
Cupressus arizonica	0	1		nd	nd	nd	
Cupressus macrocarpa	0	1		nd	nd	nd	
Cupressus sempervirens	0	1		1	nd	nd	Sansford *et al.*, 2009, Moralejo *et al.*, 2009
Elaeagnus angustifolia	0	1		nd	nd	nd	
Eucalyptus robusta	0	1		nd	nd	nd	
Eucalyptus viminalis	0	1		1	2	2	Ireland *et al.*, 2011, 2012
Fraxinus ornus subsp. ornus	0	1		nd	1	nd	Sansford *et al.*, 2009
Ilex aquifolium	1	1	F	1	1	nd	Sansford *et al.*, 2009
Juniperus thurifera	0	1		nd	nd	nd	
Laurus nobilis	1	1	F	1	1	1	Sansford *et al.*, 2009
Liquidambar styraciflua	0	1		nd	nd	nd	
Liriodendron tulipifera	0	1		1	nd	nd	Sansford *et al.*, 2009
Morus alba	0	1		nd	nd	nd	
Morus nigra	0	1		nd	nd	nd	
Olea europaea	0	1		1	nd	nd	Moralejo *et al.*, 2009
Ostrya carpinifolia	0	1		nd	nd	nd	
Pinus mugo subsp. uncinata	0	1		nd	nd	nd	
Pinus strobus	0	1		nd	nd	nd	
Platanus orientalis	0	1		nd	nd	nd	
Platanus x hispanica	0	1		nd	nd	nd	
Populus alba	0	1		nd	nd	nd	
Populus deltoides	0	1		nd	nd	nd	
Populus x canadensis	0	1		nd	nd	nd	
Populus x canescens	0	1		nd	nd	nd	
Prunus cerasifera	0	1		nd	nd	nd	
Prunus lusitanica	1	1	F	1	1	nd	Sansford *et al.*, 2009
Prunus padus	0	1		nd	nd	nd	
Prunus serotina	0	1		nd	nd	nd	
Quercus crenata	0	1		nd	nd	nd	
Quercus falcata	1	1	T	2	nd	nd	Sansford *et al.*, 2009
Quercus palustris	0	1		2	1	nd	Sansford *et al.*, 2009
Quercus pyrenaica	0	1		nd	nd	nd	
Rhamnus cathartica	1	1	F	nd	nd	nd	Ivors *et al.*, 2006
Salix alba	0	1		1	2	nd	Sansford *et al.*, 2009
Salix atrocinerea	0	1		nd	nd	nd	
Salix caprea	1	1	F	nd	1	nd	Sansford *et al.*, 2009
Salix daphnoides	0	1		nd	nd	nd	
Salix fragilis	0	1		nd	nd	nd	

Salix pentandra	0	1		nd	nd	nd	
Salix x rubens	0	1		nd	nd	nd	
Sequoia sempervirens	1	1	FB	1	2	1	Sansford *et al.*, 2009
Sequoiadendron giganteum	1	1	FB	1	nd	nd	Sansford *et al.*, 2009
Sorbus aria	0	1		nd	nd	nd	
Sorbus aucuparia subsp. aucuparia	1	1	?	1	1	nd	Sansford *et al.*, 2009
Sorbus latifolia	0	1		nd	nd	nd	
Sorbus mougeotii	0	1		nd	nd	nd	
Taxodium distichum	0	1		nd	1	nd	Preuett *et al.*, 2013
Taxus baccata	1	1	FB	2	2	1	Sansford *et al.*, 2009, DEFRA 2004
Thuja occidentalis	0	1		nd	nd	nd	
Thuja plicata	0	1		1	1	nd	Sansford *et al.*, 2009
Tilia x europaea	0	1		nd	nd	nd	
Tsuga heterophylla	1	1	FB	2	2	nd	Sansford *et al.*, 2009
Ulmus laevis	0	1		nd	nd	nd	
Ulmus minor	0	1		1	1	nd	Sansford *et al.*, 2009
Ulmus procera	0	1		1	2	2	Sansford *et al.*, 2009, Denman *et al.*, 2006

Table 4: Vulnerability and competence regarding *Phytophthora ramorum* of regulated tree species in France (species in bold are commented on in the text)

Latin name	Common name	Vulnerability	Uncertainty	Competence	Uncertainty
Abies alba Mill.	European silver fir	Low to moderate	High	Not determined	No data
Abies bornmuelleriana Mattf.C	Turkish fir	Not determined	No data	Not determined	No data
Abies cephalonica Loud.	Greek fir	Not determined	No data	Not determined	No data
Abies grandis Lindl.	Grand fir	Moderate to high	Moderate	Low/Not significant	Low
Abies pinsapo Boiss.	Spanish fir	Not determined	No data	Not determined	No data
Acer campestre L.	Field maple	Low/Not significant	Moderate	Low/Not significant	Moderate
Acer platanoides L.	Norway maple	Low to moderate	High	Not determined	No data
Acer pseudoplatanus L.	Sycamore	Low to moderate	Moderate	Low/Not significant	Moderate
Alnus cordata (Loisel.) Duby.	Italian alder	Not determined	No data	Not determined	No data
Alnus glutinosa Gaertn.	European alder, black alder	Low/Not significant	Low	Low/Not significant	Low
Alnus incana Moench.	Grey alder	Low/Not significant	Moderate	Not determined	No data
Betula pendula Roth	Silver birch	Low to moderate	Low	Low/Not significant	Low

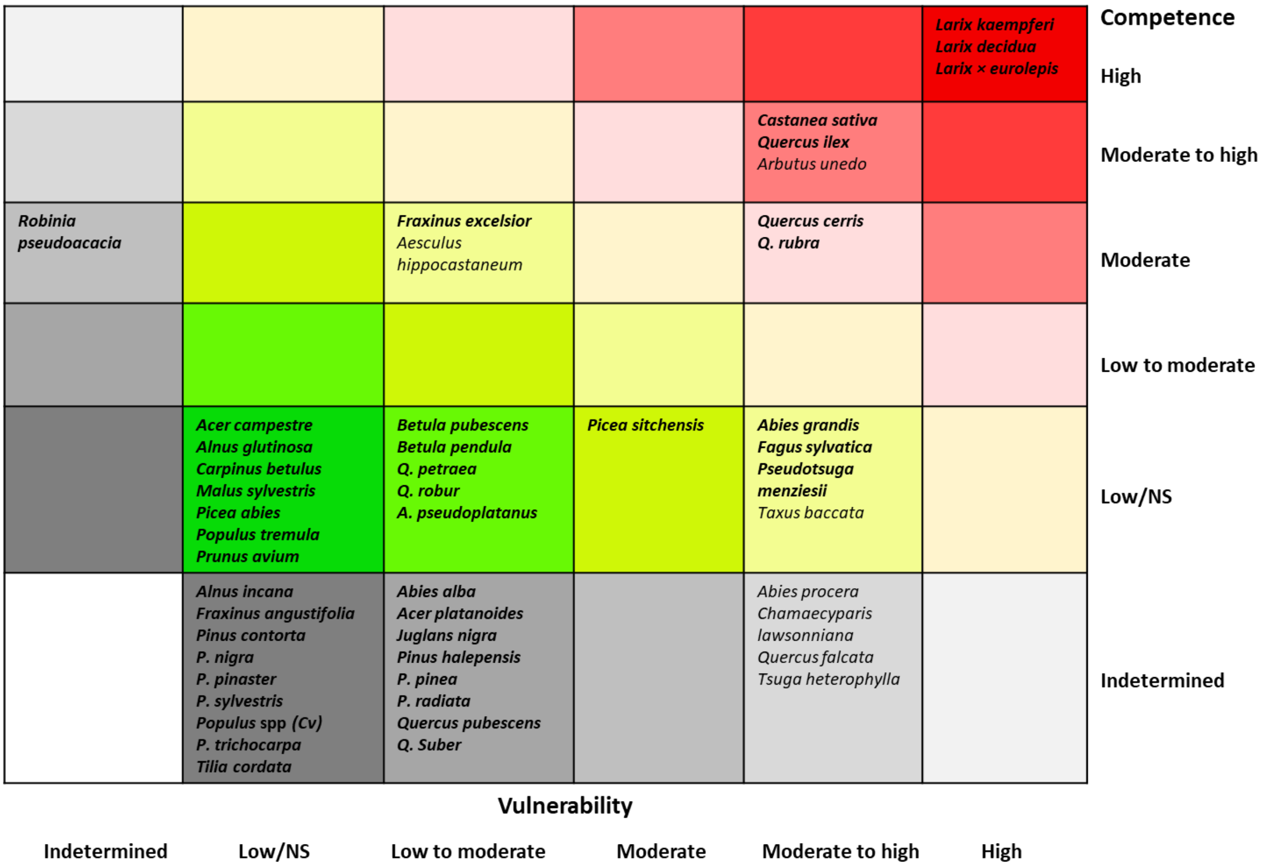
Betula pubescens Ehrh.	White birch	Low to moderate	Low	Low/Not significant	Low
Carpinus betulus L.	Hornbeam	Low/Not significant	Low	Low/Not significant	Low
Castanea sativa Mill.	Sweet chestnut	Moderate to high	Moderate	Moderate to high	Moderate
Cedrus atlantica Carr.	Atlas cedar	Not determined	No data	Not determined	No data
Cedrus libani A. Richard	Cedar of Lebanon	Not determined	No data	Not determined	No data
Eucalyptus globulus Labill.	Tasmanian blue gum	Not determined	No data	Not determined	No data
Eucalyptus gunnii Hook.f and hybrids	Cider gum tree	Not determined	No data	Not determined	No data
Fagus sylvatica L.	Beech	Moderate to high	Low	Low/Not significant	Low
Fraxinus angustifolia Vahl.	Narrow-leaved ash	Low/Not significant	Moderate	Not determined	No data
Fraxinus excelsior L.	Common ash	Low to moderate	Low	Moderate	Moderate
Juglans nigra L.	Black walnut	Low to moderate	High	Not determined	No data
Juglans regia L. and hybrids	English walnut, common walnut	Not determined	No data	Not determined	No data
Larix decidua Mill.	European larch	High	Moderate	High	Moderate
Larix kaempferi Carr.	Japanese larch	High	Low	High	Low
Larix sibirica Ledeb.	Siberian larch	Not determined	No data	Not determined	No data
Larix x eurolepis Henry	Hybrid larch	High	Moderate	High	Moderate
Malus sylvestris Mill.	Crab apple	Low/Not significant	Moderate	Low/Not significant	Low
Picea abies Karst.	Norway spruce	Low/Not significant	Low	Low/Not significant	Low
Picea sitchensis Carr.	Sitka spruce	Moderate	Low	Low/Not significant	Low
Pinus brutia Ten.	Turkish pine	Not determined	No data	Not determined	No data
Pinus canariensis C. Smith	Canary Island pine	Not determined	No data	Not determined	No data
Pinus cembra L.	Swiss stone pine	Not determined	No data	Not determined	No data
Pinus contorta Loud.	Lodgepole pine	Low/Not significant	Moderate	Not determined	No data
Pinus halepensis Mill.	Aleppo pine	Low to moderate	Moderate	Not determined	No data
Pinus leucodermis Antoine	Bosnian pine	Not determined	No data	Not determined	No data
Pinus nigra Arn.	Black pine	Low/Not significant	Moderate	Not determined	No data
Pinus pinaster Aït	Maritime pine	Low/Not significant	Moderate	Not determined	No data

Pinus pinea L.	Stone pine, parasol pine	Low to moderate	Moderate	Not determined	No data
Pinus radiata D. Don	Monterey pine	Low to moderate	Moderate	Not determined	No data
Pinus sylvestris L.	Scots pine	Low/Not significant	Low	Not determined	No data
Pinus taeda L.	Loblolly pine	Not determined	No data	Not determined	No data
Populus nigra L.	European black poplar	Not determined	No data	Not determined	No data
Populus ssp.	hybrid cultivars	Low/Not significant	Moderate	Not determined	No data
Populus tremula L.	Aspen	Low/Not significant	High	Low/Not significant	Low
Populus trichocarpa L.	Western balsam poplar	Low/Not significant	Moderate	Not determined	No data
Prunus avium L.	Wild cherry	Low/Not significant	High	Low/Not significant	Low
Pseudotsuga menziesii (Mirb.) Franco	Douglas fir	Moderate to high	Low	Low/Not significant	Low
Quercus cerris L.	Turkey oak	Moderate to high	Moderate	Moderate	Moderate
Quercus ilex L.	Holm oak	Moderate to high	Moderate	Moderate to high	Moderate
Quercus petraea Liebl.	Sessile oak	Low to moderate	Low	Low/Not significant	Low
Quercus pubescens Willd.	Downy oak	Low to moderate	High	Not determined	No data
Quercus robur L.	English oak, pedunculate oak	Low to moderate	Low	Low/Not significant	Low
Quercus rubra L.	Northern red oak	Moderate to high	Moderate	Moderate	Moderate
Quercus suber L.	Cork oak	Low to moderate	High	Not determined	No data
Robinia pseudoacacia L.	False acacia, black locust	Not determined	No data	Moderate	High
Sorbus domestica L.	Service tree	Not determined	No data	Not determined	No data
Sorbus torminalis L.	Wild service tree	Not determined	No data	Not determined	No data
Tilia cordata Mill.	Small-leaved lime, small-leaved linden	Low/Not significant	Moderate	Not determined	No data
Tilia platyphyllos Scop	Large-leaved lime, large-leaved linden	Not determined	No data	Not determined	No data

Table 5: Vulnerability and competence regarding *Phytophthora ramorum* of unregulated tree species in France (species in bold are commented on in the text)

Latin name	Vulnerability	Uncertainty	Competence	Uncertainty
Abies nordmanniana	Not determined	No data	Not determined	No data
Abies procera	Moderate to high	Moderate	Not determined	No data
Acer monspessulanum	Low/Not significant	Moderate	Not determined	No data
Acer negundo	Not determined	No data	Not determined	No data
Acer opalus subsp. opalus	Not determined	No data	Not determined	No data
Aesculus hippocastanum	Low to moderate	Moderate	Moderate	Moderate
Ailanthus altissima	Not determined	No data	Not determined	No data
Arbutus unedo	Moderate to high	Moderate	Moderate to high	Moderate
Cedrus deodara	Not determined	No data	Not determined	No data
Celtis australis	Low/Not significant	Moderate	Not determined	No data
Cercis siliquastrum	Low/Not significant	Moderate	Not determined	No data
Chamaecyparis lawsoniana	Moderate to high	Moderate	Not determined	No data
Corylus avellana	Low/Not significant	Moderate	Not determined	No data
Crataegus laevigata	Not determined	No data	Not determined	No data
Crataegus monogyna	Low/Not significant	Moderate	Low/Not significant	Moderate
Cryptomeria japonica	Not determined	No data	Not determined	No data
Cupressus arizonica	Not determined	No data	Not determined	No data
Cupressus macrocarpa	Not determined	No data	Not determined	No data
Cupressus sempervirens	Low/Not significant	Moderate	Not determined	No data
Elaeagnus angustifolia	Not determined	No data	Not determined	No data
Eucalyptus robusta	Not determined	No data	Not determined	No data
Eucalyptus viminalis	Low/Not significant	Moderate	Moderate	High
Fraxinus ornus subsp. ornus	Not determined	No data	Not determined	No data
Ilex aquifolium	Moderate to high	Low to moderate	Low/Not significant	High
Juniperus thurifera	Not determined	No data	Not determined	No data
Laurus nobilis	Low to moderate	Moderate	Low/Not significant	Moderate
Liquidambar styraciflua	Not determined	No data	Not determined	No data
Liriodendron tulipifera	Low/Not significant	Moderate	Not determined	No data
Morus alba	Not determined	No data	Not determined	No data
Morus nigra	Not determined	No data	Not determined	No data
Olea europaea	Low/Not significant	Moderate	Not determined	No data
Ostrya carpinifolia	Not determined	No data	Not determined	No data
Pinus mugo subsp. uncinata	Not determined	No data	Not determined	No data
Pinus strobus	Not determined	No data	Not determined	No data
Platanus orientalis	Not determined	No data	Not determined	No data

Platanus x hispanica	Not determined	No data	Not determined	No data
Populus alba	Not determined	No data	Not determined	No data
Populus deltoides	Not determined	No data	Not determined	No data
Populus x canadensis	Not determined	No data	Not determined	No data
Populus x canescens	Not determined	No data	Not determined	No data
Prunus cerasifera	Not determined	No data	Not determined	No data
Prunus lusitanica	Low to moderate	High	Low/Not significant	High
Prunus padus	Not determined	No data	Not determined	No data
Prunus serotina	Not determined	No data	Not determined	No data
Quercus crenata	Not determined	No data	Not determined	No data
Quercus falcata	Moderate to high	Moderate	Not determined	No data
Quercus palustris	Low to moderate	High	Not determined	No data
Quercus pyrenaica	Not determined	No data	Not determined	No data
Rhamnus cathartica	Low to moderate	High	Low/Not significant	High
Salix alba	Low/Not significant	Moderate	Not determined	No data
Salix atrocinerea	Not determined	No data	Not determined	No data
Salix caprea	Low to moderate	High	Low/Not significant	High
Salix daphnoides	Not determined	No data	Not determined	No data
Salix fragilis	Not determined	No data	Not determined	No data
Salix pentandra	Not determined	No data	Not determined	No data
Salix x rubens	Not determined	No data	Not determined	No data
Sequoia sempervirens	Low to moderate	Moderate	Low/Not significant	Moderate
Sequoiadendron giganteum	Low to moderate	Moderate	Low/Not significant	High
Sorbus aria	Not determined	No data	Not determined	No data
Sorbus aucuparia subsp. aucuparia	Low to moderate	High	Not determined	No data
Sorbus latifolia	Not determined	No data	Not determined	No data
Sorbus mougeotii	Not determined	No data	Not determined	No data
Taxodium distichum	Not determined	No data	Not determined	No data
Taxus baccata	Moderate to high	Moderate	Low/Not significant	Moderate
Thuja occidentalis	Not determined	No data	Not determined	No data
Thuja plicata	Low/Not significant	Moderate	Not determined	No data
Tilia x europaea	Not determined	No data	Not determined	No data
Tsuga heterophylla	Moderate to high	Moderate	Not determined	No data
Ulmus laevis	Not determined	No data	Not determined	No data
Ulmus minor	Low/Not significant	Moderate	Not determined	No data
Ulmus procera	Low/Not significant	Moderate	Moderate	High



Competence \ Vulnerability	Indetermined	Low/NS	Low to moderate	Moderate	Moderate to high	High
High						***Larix kaempferi*** ***Larix decidua*** ***Larix × eurolepis***
Moderate to high					***Castanea sativa*** ***Quercus ilex*** *Arbutus unedo*	
Moderate	***Robinia pseudoacacia***		***Fraxinus excelsior*** *Aesculus hippocastaneum*		***Quercus cerris*** ***Q. rubra***	
Low to moderate						
Low/NS		***Acer campestre*** ***Alnus glutinosa*** ***Carpinus betulus*** ***Malus sylvestris*** ***Picea abies*** ***Populus tremula*** ***Prunus avium***	***Betula pubescens*** ***Betula pendula*** ***Q. petraea*** ***Q. robur*** ***A. pseudoplatanus***	***Picea sitchensis***	***Abies grandis*** ***Fagus sylvatica*** ***Pseudotsuga menziesii*** *Taxus baccata*	
Indetermined		***Alnus incana*** ***Fraxinus angustifolia*** ***Pinus contorta*** ***P. nigra*** ***P. pinaster*** ***P. sylvestris*** ***Populus spp (Cv)*** ***P. trichocarpa*** ***Tilia cordata***	***Abies alba*** ***Acer platanoides*** ***Juglans nigra*** ***Pinus halepensis*** ***P. pinea*** ***P. radiata*** ***Quercus pubescens*** ***Q. Suber***		*Abies procera* *Chamaecyparis lawsonniana* *Quercus falcata* *Tsuga heterophylla*	

Figure 11: Classification of susceptibility (competence and vulnerability) to *Phytophthora ramorum* of regulated forest tree species in France (in bold) and of a few other unregulated species (NS = not significant). Species for which both components are undetermined have not been included. Many uncertainties are moderate or high, read the text for more details.

Details on the species with the highest vulnerability and/or competence

- **The three larch species (*Larix kaempferi, L. decidua and L. x eurolepis*)** combine high vulnerability and competence, with low uncertainty for Japanese larch but moderate uncertainty (for both criteria) for European and hybrid larch.

The very high susceptibility of Japanese larch (*L. kaempferi*) is demonstrated by the epidemic observed in the United Kingdom since 2009 (Brasier and Webber, 2010; Webber *et al*., 2010) and then in Ireland. *L. kaempferi* is an important plantation species in Great Britain, constituting the largest proportion of the 130,000 ha of larch tree stands. Symptoms caused by *P. ramorum* affect all tree organs, with needle discolouration and loss, aborted bud flush, wilting of shoots, and extensive resin bleeding and cortical lesions on trunks (Webber *et al.,* 2010). Mortality of infected trees is often observed within two to three years. Infection of *L. decidua* and *L. x eurolepis* by *P. ramorum* was reported a few months after *L. kaempferi* (Forestry Commission, 2011, in: Palmieri *et al*., 2011). Since then, all surveillance data (based on helicopter remote sensing with field validation) have been combined for the three species. From 2010 to 2018, more than 16,000 ha of larch trees (12% of the standing volume) were cut down due to infection by *P. ramorum*, with a high proportion in Wales before 2014, and more recently in Scotland (Forestry Commission, 2018).

Much of the scientific literature data on the susceptibility of *L. decidua* and *L. eurolepis* comes from Anna Harris' thesis (2015), supervised by Joan Webber and Simon Archer. The content of this thesis has been partially published in three papers (King *et al*., 2015; Harris and Webber, 2016; Harris *et al*., 2018).

Concerning natural infections, *P. ramorum* was observed on *L. decidua* and *L. eurolepis* in Great Britain from 2011 (Palmieri *et al*., 2011), producing the same symptoms as on *L. kaempferi*, i.e. needle loss, branch mortality and cankers with resin bleeding on trunks, which can lead to mortality. A. Harris verified Koch's postulates for all three species. Although annual surveillance campaigns have been carried out since discovery of the disease, there are no quantified data on prevalence, incidence or severity by larch species. Based on the list of isolates obtained from these field campaigns, there are proportionately fewer isolates from European larch than from Japanese larch: 2.8% of the total for the "historical" collection from 2002-2012 (King *et al*., 2015) and 0.6% for the period 2009-2013 (Harris, 2015, page 114), whereas the European larch probably accounts for about 17% of larch plantations in Great Britain (Harris, 2015). However, the two species of larch have slightly different ecological preferences and geographical distribution, which could explain a different exposure to the pathogen. Only one comparative study under natural conditions was carried out at a site in south-west England (Wiltshire) in 2010-2011, comprising two plots: one with 70% *L. kaempferi*, another with 70% *L. decidua.* A. Harris reported that the disease in European larch was less severe than in Japanese larch, in terms of symptoms (visible mainly on the trunks) and number of infected trees (page 120). On the other hand, while *P. ramorum* was re-isolated from 67% of *L. kaempferi* litter samples, only 2% of samples were positive for the European larch stand (page 124). These few observations under natural conditions may therefore suggest lower susceptibility of *L. decidua* compared to *L. kaempferi*, both on trunks and needles. However, data are scarce, partial and potentially affected by sampling bias. In addition, the genetic nature of the material may be uncertain: some stands of "Japanese larch" from seeds harvested in Great Britain may have a certain proportion of hybrids with European larch (Lines, 1987).

The three species of larch were compared in artificial inoculation tests. A. Harris conducted five experiments, at different times of the year, on logs with wounds and leafy shoots without wounds, with several isolates (from groups EU1 and NA2) and several measured variables (severity of symptoms, re-isolation rate and sporulation as sporangia and chlamydospores on needles). In all cases, the susceptibility of *L. decidua* was not significantly different or was sometimes greater than that of *L. kaempferi* (pages 78, 82, 84, 90, 92, 98, 108, 112, 118, 149, 152, 170, in Harris' thesis (2015); Harris and Webber, 2016). These results are consistent with those of Chastagner *et al*. (2013), which show equivalent susceptibility of *L. decidua* and *L. kaempferi*, intermediate between *L. occidentalis*, which is even more susceptible, and *L. laricina*, which is less susceptible, after inoculation by spraying zoospores on plants or branches, repeated over two years, with three isolates belonging to the NA1, NA2 and EU1 lineages. Compared to other species considered highly susceptible at the foliar level (*Umbellularia californica*, blueberry and rhododendron), the three larch species showed the highest levels of sporulation but a far lower symptom expression and re-isolation rate (Harris and Webber, 2016).

Anna Harris concluded (page 173) that European and hybrid larch should not be considered as alternatives to Japanese larch because the bark of all three species is equally susceptible (as shown in laboratory testing) and because their needles support high levels of sporulation. We questioned J. Webber, who maintains this analysis. After a period of differentiated control measures in 2010-2011 (elimination of only symptomatic trees for European larch, compared with clearcutting of infected stands of Japanese larch, Harris (2015), p. 120) the three larch species are now subject to the same recommendations, in terms of eradication or risks for planting in Great Britain.

Harris noted, however, that although susceptibility was generally similar between *Larix* species, certain traits could lead to differences. Thus, the presence of five stomatal bands on Japanese larch needles instead of one to three for European larch could facilitate the production of sporangia (page 95). Conversely, the lower concentration of tannins and phenols in the bark of European larch compared to Japanese larch could favour the development of *P. ramorum* in tissues, especially at the end of the season (page 113), while direct penetration of zoospores into the bark seems to be lower than for Japanese larch. These mechanisms remain hypothetical and require further study. Lastly, A. Harris stressed that more research is required about within-species genetic variation. **Indeed, this is the main limitation of her study, in which each of the larch species was represented by only two or three individuals in each of the trials.** *L. decidua* is known to have high intra-species variability for several traits (particularly disease resistance) depending on the regions of origin in its fragmented natural area (Alps, Sudetenland) (Jansen and Geburek, 2016; Wagner *et al*., 2015 a and b).

- **Sweet chestnut (*Castanea sativa*)** has moderate to high vulnerability and competence, both with moderate uncertainty.

The first infections on sweet chestnut (*Castanea sativa*) were observed on leaves from stumps sprouts and epicormic shoots in Cornwall in 2003 (Denman *et al.*, 2005b). At that time, the main identified sources of inoculum were rhododendrons, and infections were limited to leaves from the lower part of the crown, with cankers on trunks rarely being observed (Webber *et al*., 2017). After 2009 and the start of the larch epidemic, sweet chestnut infections were more frequently observed in the vicinity of larch outbreaks (Webber *et al*., 2010). Due to their multiplicity, foliar infections in the crown can lead to significant defoliation, with necrosis of petioles and twigs being observed. The symptoms described correspond to a progressive crown dieback. The perennity of tree infections is believed to be ensured by the mycelium overwintering in buds and cortical tissues (Webber *et al*., 2017). Recent observations now suggest that an epidemic on sweet chestnut is developing independently of the presence of larch (Webber *et al*., 2017). More than 50 sites of declining sweet chestnut (where the role of *P. cinnamomi* or *P. cambivora* was initially suspected) have been studied in the south west of England, relatively far from infected larch (>2 km) and without rhododendron in the understory. It appears that more than two-thirds of these sites are infected by *P. ramorum*, with sometimes a high prevalence, and some trees showing symptoms of severe dieback combined with bark necrosis and girdling of the main branches. So far, no eradication measures have been put in place for sweet chestnut outbreaks. Only some trees, generally the most infected and potentially dangerous ones, have been cut down (personal communication, M. Biddle, Forestry Commission, August 2018). The south west of England is not an area where sweet chestnut is exploited as a forest species, and the infected sites correspond to "semi-natural woodlands". However, the question of the management of infected sweet chestnut outbreaks now arises (Webber *et al.*, 2017).

Despite infections being observed under natural conditions, there are still uncertainties about the levels of sweet chestnut vulnerability and competence, which were deemed here as moderate. The assessment of sweet chestnut susceptibility clearly illustrates the difficulty of completely dissociating vulnerability and competence, and of estimating these components of susceptibility in an epidemic context with increasing inoculum pressure. Until recently, observations in Great Britain may have suggested moderate vulnerability and non-significant competence. With the increase in inoculum produced by larch, some infections in the sweet chestnut canopy may have occurred (despite a low elementary probability of long-distance dispersal), revealing significant competence and further accelerating inoculum production in the crowns of trees, with more and more negative impacts (Webber *et al*., 2017). However, the contribution of *P. ramorum* to the chestnut decline has yet to be clarified, possibly in interaction with other factors. The effects of age (affected trees in England are often old trees) and of management (for forestry or fruit production) should be considered, particularly under conditions where stands are managed as high or low forest (conditions that may favour the development of the disease). In addition, interactions between *P. ramorum* and other pathogens could also affect the vulnerability of this species. Under natural conditions, leaf necrosis does not systematically spread to stems and branches, suggesting low susceptibility of cortical tissue (but contradicting branch mortality). After controlled inoculations on detached leaves and logs, the susceptibility of sweet chestnut was considered moderate (Denman *et al*., 2005a; Sansford *et al*., 2009). With regard to competence, sweet chestnut enables *P. ramorum* to sporulate at a level that does not differ significantly from rhododendron and California bay laurel under controlled conditions, although it is lower than larch (Harris and Webber, 2016; Webber *et al*., 2017). Leaf symptom expression was comparable to that of rhododendron (greater than that of California bay laurel) and a positive correlation was observed between the percentage of leaf area infected and sporangia production (in May and October) (Harris and Webber, 2016). However, the temporal dynamics of sporangia production (peak sporulation in August) and the high variability in the number of sporangia produced (possibly related to a "tree" effect) can affect the reproducibility of these results. In addition, it is likely that the role of sweet chestnut in the spread of *P. ramorum* also depends on the environmental conditions prevailing before leaf drop, and on the viability of the inoculum present on the leaves on the ground and in litter. To predict and manage the "*P. ramorum*" risk for the chestnut and forestry sectors, it also seems necessary to study the vulnerability and competence of Asian sweet chestnut species and inter-species hybrids, which represent a significant proportion of the chestnut fruit varieties used in France, and on which there are no data.

- The question of the susceptibility of **European oaks** to *P. ramorum* has been raised ever since SOD was first described in California. There have been only sporadic reports on oaks so far in Europe.

However, vulnerability and competence were considered moderate to high for the holm oak, ***Quercus ilex***. Despite the relatively low abundance of this species in Great Britain, natural infections have been observed with a relatively high incidence, in the form of foliar symptoms associated with branch mortality, in forests, parks and gardens, and nurseries (Denman *et al*., 2005a; King *et al*., 2015). Laboratory studies showed very high leaf susceptibility, associated with high sporulation for this species (Denman *et al*., 2005a and 2006). Under controlled infection conditions, 70% of inoculated young plants expressed symptoms and allowed sporulation (Denman *et al*., 2008). Latent or non-symptomatic infections associated with sporangia production were also observed after exposure to a natural inoculum *in situ* (Denman *et al*., 2006), thus confirming the competence of this host. However, there are still uncertainties about the susceptibility of holm oaks (vulnerability and competence) outside Great Britain, in areas where they are naturally abundant and subject to a different climate, for example, in France and Spain (Moralejo *et al.*, 2006 and 2009).

On ***Q. cerris***, symptoms have been observed on leaves and trunks in England, but no symptoms of branch mortality (FERA, 2015). Leaf susceptibility has been proven under controlled conditions but is lower and with lower sporulation than for *Q. ilex* (Denman *et al*., 2005a and 2006), resulting in its competence being estimated as moderate.

Vulnerability and competence were considered respectively moderate to high and moderate for Northern red oak ***Q. rubra***. Some natural infections with bleeding cankers have been observed in the vicinity of infected rhododendron (Netherlands). The relatively high susceptibility of cortical tissues of the trunk and branches was confirmed after inoculation under controlled conditions (Brasier *et al.,* 2002; de Gruyter *et al*., 2002; Tooley and Kyde, 2007). *Q. rubra* has relatively low leaf susceptibility in terms of symptoms (Denman *et al*., 2005a and 2006; Tooley *et al*., 2011; Jinek *et al*., 2011) although high sporulation can be observed (Tooley *et al.*, 2011). As this species is relatively scarce in the areas currently affected by *P. ramorum* epidemics (Western North America, Great Britain), uncertainties remain about its susceptibility (vulnerability and competence).

After the SOD epidemic, ***Q. robur* and *Q. petraea*** became the focus of particular surveillance due to their leading importance in Europe. Under this careful surveillance, very few natural infections have been observed, and only a few rare reports of bleeding cankers associated with *P. ramorum* have been mentioned in Great Britain (FERA, 2015). Although symptoms have been observed in susceptibility tests under controlled conditions on logs and leaves (Brasier *et al*., 2002; Denman *et al*., 2005a and 2006), it was concluded that these two species had low to moderate vulnerability to *P. ramorum.* Similarly, as no foliar infections have been reported so far despite the likely high exposure of these species to *P. ramorum* inoculum in Great Britain, the competence of these species has been assessed as not significant, even though *P. ramorum* sporulation has been observed on leaves after inoculation, at a much lower level than for *Q. ilex* and *Q. cerris* (Denman *et al*., 2006).

The moderate uncertainty of these assessments for the two species lies in: 1) the risks of non-detection of foliar symptoms, which may be discrete under natural conditions, particularly for *Q. robur*, which expresses few foliar symptoms after inoculation of leaves under laboratory conditions; 2) the non-reproducibility of *P. ramorum* sporulation measurements on leaves of these oaks: in some studies sporulation was significant, in others not significant.

- Bleeding cortical cankers are frequently observed on ***Fagus sylvatica*** in England, and cortical tissues also seem highly susceptible to *P. ramorum* in inoculations.

Foliar infections have been observed (FERA, 2015) but sporulation of *P. ramorum in vitro* is not significant. Consequently, the competence of *F. sylvatica* is not regarded as significant. The behaviour of beech should be compared to that of *Q. agrifolia*, which in California does not participate in the effective transmission of the inoculum and only has major symptoms in the presence of competent hosts, California bay laurel and tanoak (*Notholithocarpus densiflorus*).

- ***Fraxinus excelsior*** is widespread in England and therefore highly exposed to the inoculum. Only leaf infections have been reported, with no branch mortality or trunk symptoms, leading to its vulnerability being estimated as low to moderate.

However, there is uncertainty due to the high prevalence of ash dieback in England, which could increase the risk of misdiagnosis and possibly underestimate the contribution of *P. ramorum*.

Competence was deemed to be moderate in the absence of a natural epidemic but considering the high leaf susceptibility and high levels of sporulation observed in the laboratory (Denman *et al.*, 2005a, 2006). However, again, the uncertainty comes from the possible interference with ash dieback. In addition, it was mentioned to us that the rapid defoliation induced by *P. ramorum* on common ash may severely limit its competence (J. Webber, personal communication).

Within the same genus, data on ***F. angustifolia*** are far more incomplete; in particular, there are no sporulation data.

- The **black locust (false acacia)** *Robinia pseudoaccacia* is not described as a natural host of *P. ramorum* but this species is not very common in Great Britain.

Under controlled conditions, it showed high leaf susceptibility and *P. ramorum* sporulation levels (Tooley and Browning, 2009; Bulajic *et al*., 2010), leading to it being classified with "moderate competence", albeit with high uncertainty.

- **Douglas fir** *(Pseudotsuga menziesii*) has moderate to high vulnerability, but no significant competence.

This species' behaviour is fairly well documented due to its widespread presence in the western United States, particularly in areas contaminated by *P. ramorum* (Ramage *et al*., 2012; Forrestel *et al*., 2015). Despite its high exposure under natural conditions and quite high susceptibility in tests with inoculations on shoots or logs (Hansen *et al*., 2005), little damage has been reported on Douglas fir. Notable symptoms, mainly wilting of the current season's shoots (comparable to the effect of a late frost), have only been observed in situations with very high inoculum pressure, usually under the canopy of tanoaks (*Notholithocarpus densiflorus*) or near heavily infected California bay laurel, and rather on seedlings (Hansen *et al*., 2008; Chastagner *et al*., 2008). This may be partly explained by the fact that Douglas fir is only susceptible for a short period of time in the spring, at bud break (Hansen *et al*., 2005). In addition, high inoculum pressure is required to obtain symptoms (Chastagner *et al*., 2013). Damage to Douglas fir and **grand fir** (*Abies grandis*), whose behaviour appears to be quite similar to that of Douglas fir, has been reported in Christmas tree plantations in California, where shoot dieback can have a direct economic impact (shape defects) (Chastagner *et al*., 2008). **Sitka spruce** appears to have the same type of behaviour as Douglas fir and grand fir, with reports of current season's shoot dieback but no sporulation (Denman *et al*., 2005a; DEFRA, 2005; Forestry Commission, 2017).

- Among unregulated species, the moderate to high competence of the **strawberry tree** (*Arbutus unedo*) and **horse chestnut** (*Aesculus hippocastaneum*) should be mentioned.

These two species allow high sporulation of *P. ramorum in vitro* (Moralejo *et al*., 2006; Sansford *et al*., 2009). In particular, the strawberry tree could play a significant role in certain environments in the south of France where it is relatively abundant. Reports of infected strawberry trees in nurseries have been provided by Spain and England (EPPO, 2013).

- The **Lawson cypress** (*Chamaecyparis lawsoniana*) was found naturally infected by *P. ramorum* in England in windbreaks (shelterbreaks) showing symptoms of dieback (Brasier and Webber, 2012).

There are no data on its potential competence (Forestry Commission, 2017). In Brittany, Lawson cypress was found to be highly susceptible to *P. lateralis*, a species closely related to *P. ramorum* that can also produce aerial infections (Robin *et al*., 2011). It is therefore necessary to be vigilant for this species.

3.5.3 Shrubs

The competence of shrub species was systematically estimated to be a level below that of tree species with comparable inoculum production per unit of leaf area. This is justified by the fact that the height of the infected individuals determines to a certain extent the distance at which the inoculum can be dispersed: around a dozen metres for rhododendron, but around a hundred metres for larch (Brasier and Jung, 2006). Only *Rhododendron ponticum* has been estimated to have moderate to high competence, but it is very uncommon in French forests (Table 6). A few other frequent species have been estimated to have low to moderate competence: heather (*Calluna vulgaris*), blueberry (*Vaccinium myrtillus*), viburnum (*Viburnum tinus*) and lilac (*Syringa vulgaris*).

Uncertainties regarding the competence of understory species are often moderate to high (with an absence of data in some cases). Experimental data are sometimes difficult to interpret with, for example, very high sporangia densities obtained by relating a small number of observed sporangia to extremely small lesions, such as with ivy, bramble and, to a lesser extent, honeysuckle (*Lonicera periclymenum*) and dog rose (*Rosa canina*) (DEFRA 2004). This is a problem, precisely because the California bay laurel, *Umbellularia californica,* recognised as the most competent species in the western United States, has small leaf lesions with high sporulation per unit area of lesion.

Table 6: Competence regarding *Phytophthora ramorum* of the most frequent shrub species in French forests (some infrequent but significantly competent species have been included)

Species	Height	Type	Number of observations	Natural infection	Leaf suscep-tibility	Sporu-lation	Competence	Uncertainty	References
Amelanchier ovalis	2-4m	Deciduous	4149	0	nd	nd	Not determined	No data	
Buxus sempervirens	4-8m	Evergreen	5720	No	1	nd	Not determined	No data	Kaminski, 2008
Calluna vulgaris	1-2m	Evergreen	8861	Yes (branches)	2	2	Low to moderate	Moderate	Kaminski, 2008, Sansford *et al.,* 2009
Cornus mas	2-4m	Deciduous	3398	0	nd	nd	Not determined	No data	
Cornus sanguinea	4-8m	Deciduous	15173	No	2	nd	Not determined	No data	Vettraino, 2008
Cytisophyllum sessilifolium	2-4m	Deciduous	1688	0	nd	nd	Not determined	No data	
Cytisus scoparius	2-4m	Deciduous	11997	Molecular detection	nd	nd	Not determined	No data	Vettraino, 2010

Daphne laureola subsp. laureola	1-2m	Evergreen	4305	0	nd	nd	Not determined	No data	
Dorycnium pentaphyllum subsp. pentaphyllum	1-2m	NA	1951	0	nd	nd	Not determined	No data	
Erica arborea	2-4m	Evergreen	1924	0	nd	nd	Not determined	No data	
Erica cinerea	1-2m	Evergreen	3823	No	2	nd	Not determined	No data	Kaminski, 2008
Erica scoparia	2-4m	Evergreen	3895	0	nd	nd	Not determined	No data	
Euonymus europaeus	2-4m	Deciduous	7956	0	nd	nd	Not determined	No data	
Genista cinerea	1-2m	NA	1627	0	nd	nd	Not determined	No data	
Genista pilosa	1-2m	NA	2458	0	nd	nd	Not determined	No data	
Hedera helix	16-32m (vine)	Evergreen	42953	Yes (stem)	1	1	Low/Not significant	Moderate	DEFRA 2004, Sansford *et al.*, 2009, FERA 2015
Hippocrepis emerus subsp. emerus	2-4m	Deciduous	1870	0	nd	nd	Not determined	No data	
Hypericum androsaemum	1-2m	Evergreen	1259	0	nd	nd	Not determined	No data	
Juniperus communis subsp. communis	4-8m	Evergreen	8700	No	2	nd	Not determined	No data	Vettraino, 2008
Juniperus oxycedrus	4-8m	Evergreen	2901	0	nd	nd	Not determined	No data	
Lavandula angustifolia subsp. angustifolia	1-2m	NA	1967	0	nd	nd	Not determined	No data	
Ligustrum vulgare	2-4m	Deciduous	15286	No	1	nd	Not determined	No data	Shishkoff, 2007
Lonicera etrusca	2-4m	Evergreen	1941	0	nd	nd	Not determined	No data	
Lonicera implexa	2-4m	Evergreen	1651	No	nd	2	Low/Not significant	Moderate	Moralejo, 2006
Lonicera periclymenum	4-8m	Deciduous	25007	No	1	2	Low/Not significant	High	DEFRA 2004, Sansford *et al.*, 2009, Swiecki & Bernhardt, 2013
Lonicera xylosteum	2-4m	Deciduous	11233	0	nd	nd	Not determined	No data	
Phillyrea angustifolia	2-4m	Evergreen	1933	0	nd	nd	Not determined	No data	
Phillyrea latifolia	4-8m	Evergreen	2427	0	nd	nd	Not determined	No data	
Pistacia lentiscus	2-4m	Evergreen	0	No	2	2	Low to moderate	Moderate	Moralejo, 2006, Sansford *et al.*, 2009
Prunus mahaleb	4-8m	Deciduous	2679	0	nd	nd	Not determined	No data	

Prunus spinosa	2-4m	Deciduous	16561	0	nd	nd	Not determined	No data	
Rhamnus alaternus	2-4m	Evergreen	2078	No	2	2	Low to moderate	Moderate	Moralejo *et al.,* 2006, Sansford *et al.,* 2009
Rhododendron ponticum	1-2m	Evergreen	0	Yes	2	2	Moderate to high	Low	Sansford *et al.,* 2009, Vercauteren, 2011
Ribes alpinum	2-4m	Deciduous	4210	0	nd	nd	Not determined	No data	
Rosa arvensis	2-4m	Deciduous	13247	0	nd	nd	Not determined	No data	
Rosa canina	2-4m	Deciduous	12818	No	1	2	Low/Not significant	High	DEFRA 2004, Vercauteren, 2011
Rubus fructicosus	2-4m	Deciduous	??	No	nd	1	Low/Not significant	Moderate	Inman, 2003
Rubus ulmifolius	2-4m	Deciduous	8567	0	nd	nd	Not determined	No data	
Ruscus aculeatus	1-2m	Evergreen	8890	0	nd	nd	Not determined	No data	
Salix cinerea	4-8m	Deciduous	2562	0	nd	nd	Not determined	No data	
Sambucus nigra	4-8m	Deciduous	8843	Yes	2	1	Low/Not significant	Moderate	DEFRA 2004, Sansford *et al.,* 2009, Vercauteren, 2011
Sambucus racemosa	2-4m	Deciduous	2909	0	nd	nd	Not determined	No data	
Smilax aspera	2-4m	Evergreen	2207	No	nd	2	Low/Not significant	High	Denman *et al.,* 2008
Staehelina dubia	0-1m	NA	1564	0	nd	nd	Not determined	No data	
Syringa vulgaris	2-4m	Deciduous	40	Yes	2	2	Low to moderate	Moderate	Beales 2004, Shishkoff 2007, Denman 2006, Sansford *et al.,* 2009

3.5.4 Ornamental species

Table 7 shows the list of ornamental species that have been reported to be infected by *P. ramorum*.

Rhododendron and viburnum are the most frequently infected species. Note the presence on this list of *Lithocarpus (syn Notholithocarpus) densiflorus* (tanoak) and *Umbellularia californica* (California bay laurel), on which the California epidemic is developing. These are sold as ornamental species in Europe and are listed in the catalogues of several French nurseries.

Table 7: List of ornamental host species of *P. ramorum*, i.e. species from which *P. ramorum* has been isolated, including the species listed in European Decision 2002/757/EC as amended 2007 (in bold) and in the lists of the Canadian Food Inspection Agency (2003), EPPO (2012) and FERA (2015)

Plant species	**Natural infections**			**Artificial inoculations**	
	Organs affected	**Pathogenicity confirmation by Koch postulates**	**References**	**Infection under controlled conditions**	**References**
Adiantum aleuticum	Leaves	YES	Vettraino *et al.*, 2006		
Adiantum jordanii	Leaves	YES	COMTF (USA)		
Aesculus californica	Leaves and branches	YES	Garbelotto *et al.*, 2003		
Aesculus hippocastanum	Trunk	YES	Forest Research	YES	Brasier *et al.*, 2002 UK PRA, 2003 *Low susceptibility on bark*
Arbutus menziesii	Leaves and branches	YES	Garbelotto *et al.*, 2003 Rizzo, 2003 COMTF		
Arbutus unedo	Leaves and branches		CSL and COMTF PRA UK, 2003	YES	Moralejo and Hernandez, 2002
***Arctostaphylos* spp.**	Leaves and branches Trunk on *A. manzanita*		COMTF, PRA, APHIS Garbelotto *et al.*, 2003	YES	Tooley & Englander, 2002, UK PRA, Inman *et al.*, 2003
Ardisia japonica	Leaves		COMTF		
Calluna vulgaris	Branches	YES	Orlikowski & Szkuta, 2004		
Calycanthus occidentalis	Leaves		COMTF		
***Camellia* spp.**	Leaves and branches, floral buds	YES	Beales *et al.,* 2004 Pintos Varela *et al.*, 2003 COMTF CFIA (Canada) PRA UK, 2003 DEFRA, 2003 Sample France 2006	YES	UK PRA, 2003 Inman *et al.*, 2003 *Highly susceptible*
Castanopsis orthacantha	Leaves and branches		Forest Research	YES	Hansen *et al.*, 2002 *Inoculation of* C. chrysophylla *logs: same level reaction as tanoak*
Ceanothus thyrsiflorus	Leaves and branches Trunk (PRA, APHIS)		COMTF	YES	Parke *et al.*, 2002 *On detached leaves of* C. impressus*: highly susceptible*
Cercis chinensis	Leaves		CFIA		
Chamaecyparis lawsoniana	Cankers		Forest Research	YES	Hansen, Sutton *et al.*, 2002 *Inoculation of logs: same level reaction as tanoak* UK PRA 2003, Brasier *et al.*, 2002 *Susceptible ("more" susceptibility)*

Choisya spp.	Leaves		NPPO Ireland, CSL	YES	UK PRA, 2003 *On leaves of* C. ternata *Practically resistant*
Corylopsis spp.	Leaves		CFIA, FERA		
Cotoneaster sp.	Leaves	YES	FERA	YES	Parke *et al.*, 2002 *On* C. multiflorus*, no symptoms on detached leaves*
Frangula californica	Leaves and branches	YES	Garbelotto *et al.*, 2003		
Frangula purshiana	Leaves	YES	Vettraino *et al.*, 2006 Goheen *et al.*, 2002		
Garrya elliptica	Branches		CSL, PRA, APHIS		
Gaultheria spp.	Leaves	YES for *G. shallon*	CFIA, CSL/FERA	YES	UK PRA, 2003 Linderman *et al.,* 2007 Inman *et al.*, 2003 *Little or no susceptibility on detached leaves*
Griselinia littoralis	Leaves and branches	YES	Giltrap *et al.*, 2004 CSL		
Hamamelis virginiana	Leaves and branches	YES	Giltrap *et al.*, 2004		
Hamamelis spp.	Leaves and branches		CSL	YES	Parke *et al.*, 2002 *Highly susceptible on detached leaves of* H. vernalis
Heteromeles arbutifolia	Leaves and branches	YES	Garbelotto *et al.*, 2003		
Hydrangea seemanni	Leaves		FERA		
Ilex spp.	Leaves		USDA, CSL/FERA, APHIS	YES	UK PRA, 2003 Linderman *et al.*, 2006 Inman *et al.,* 2003 *Not susceptible on detached leaves*
Kalmia latifolia	Leaves and branches	YES	NPPO Ireland, CSL, RAPRA UK PRA, 2003	YES	Tooley & Englander, 2002 Orlikowski & Szkuta, 2002 *Susceptible (detached leaves and...?)*
Kalmia spp.	Leaves and branches	YES	CSL, CFIA		
Laurus nobilis	Leaves	YES	CSL	YES	UK PRA, 2003 *Practically resistant*
***Leucothoe* spp.**	Leaves and branches	YES on *L. fontanesiana*	COMTF, FERA, UK PRA 2003 (*L. fontanesiana*) Sample France 2007	YES	Inman *et al.*, 2003 *Potentially highly susceptible*
Lithocarpus densiflorus	Leaves, branches and trunk	YES	Garbelotto *et al.*, 2003 Garbelotto *et al.*, 2002 Rizzo *et al.*, 2002		
Lonicera hispidula	Leaves	YES	Garbelotto *et al.*, 2003 CSL COMTF		

Magnolia spp.	Leaves and branches	YES on *Magnolia grandiflora*	FERA/CSL, APHIS, CFIA, Forest Research, COMTF, DEFRA Giltrap *et al.*, 2006		
Mahonia aquifolium	Leaves		CFIA		
Michelia doltsopa	Leaves	YES	NPPO Ireland, Forest Research, RAPRA	YES	
Michelia spp.	Leaves	YES on *M. maudiae*	CFIA, APHIS, CSL	YES	
Nerium oleander	Leaves		COMTF		
Nothofagus obliqua	Trunk		Forest Research		
Osmanthus heterophyllus	Leaves	YES	CSL, COMTF	YES	
Osmanthus spp.	Leaves and branches Trunk (PRA, APHIS)		CFIA, COMTF		
Parrotia persica	Leaves and branches	YES	Hughes *et al.*, 2006 CFIA	YES	
Photinia x fraseri	Leaves	YES	NPPO Ireland	YES	Parke *et al.*, 2002 *Detached leaves of* P. serrulata *not susceptible* Inman *et al.*, 2003 *Moderately susceptible*
***Pieris* spp.**	Leaves and branches	YES on *P. japonica x formosa,* *P. japonica,* *P. formosa,* *P. floribunda x formosa*	Parke *et al.*, 2004 Inman *et al.*, 2003 CSL, RAPRA, CFIA, NPPO Ireland, DEFRA 2003, ODA 2003 Two samples France (Finistère) 2005, 1 sample (Finistère) 2007, 1 sample 2008	YES	Tooley & Englander, 2002 UK PRA, 2003 Orlikowski & Szkuta, 2002 Inman *et al.*, 2003 *Susceptible to highly susceptible*
Pittosporum undulatum	Leaves		Hüberli *et al.*, 2006		
Prunus laurocerasus	Leaves		COMTF, FERA		UK PRA, 2003 Brasier *et al.,* 2002 *Bark: low susceptibility* *Leaf: slightly susceptible*
Prunus lusitanica	Leaves		COMTF		UK PRA, 2003 *Leaf: slightly susceptible*
Prunus spp.					Inman *et al.*, 2003 *Slightly susceptible*
***Rhododendron* spp.**	Leaves and branches	YES	DEFRA, CSL, RAPRA, COMTF, Werres *et al.*, 2001, Garbelotto *et al.*, 2003 Husson *et al.*, 2007…	YES	UK PRA, 2003 Tjosvold *et al.,* 2008 Tooley & Englander, 2002 Parke *et al.,* 2002 Inman *et al.,* 2002 *Leaves highly susceptible in general*
Ribes laurifolium	Leaves		CSL	YES	Parke *et al.*, 2002 Ribes sanguineum *leaves highly susceptible*

Rosa gymnocarpa	Leaves	YES	Hüberli *et al.*, 2004		
Rosa rugosa	Leaves		APHIS		
Rosa spp.	Leaves		APHIS	YES	Moralejo & Hernandez, 2002 *Detached leaves of* R. sempervirens *susceptible*
Rubus spectabilis	Leaves		Goheen *et al.*, 2002	YES	UK PRA, 2003 Inman *et al.*, 2003 Moralejo & Hernandez, 2002 R. fruticosus *and* R. ulmifolius *not susceptible*
Sarcococca hookeriana	Leaves and branches		SASA		
Schima argentea	Trunk		Forest Research		
Schima wallichii	Leaves, Branch tips (PRA, APHIS)		Forest Research, CSL		
Sorbus aucuparia	?		Forest Research		
Syringa vulgaris	Leaves and branches	YES	Beales *et al.*, 2004 DEFRA, 2003 Sample France 2007 on *Syringa* sp.	YES	Inman *et al.*, 2003 UK PRA, 2003 *Potentially highly susceptible*
***Taxus* spp.**	Leaves, branches and trunk	YES on *Taxus baccata*	Lane *et al.*, 2004 COMTF, CFIA Sample France 2007	YES	Brasier *et al.*, 2002 UK PRA, 2003 *Low susceptibility on bark*
Trientalis latifolia	Leaves	YES	Hüberli *et al.*, 2003		
Umbellularia californica	Leaves	YES	Garbelotto *et al.*, 2003 CSL		
Vaccinium intermedium	Leaves and branches		FERA		
Vaccinium myrtillus	Branches	YES	CSL/FERA	YES	De Gruyter *et al.*, 2002 *Susceptible (mortality of plants via leaf and stem)*
Vaccinium ovatum	Leaves and branches Trunk (PRA, APHIS)	YES	Garbelotto *et al.*, 2003 Goheen *et al.*, 2002 Storer *et al.*, 2001		
Vaccinium vitis-idaea	Leaves		CSL Orlikowski & Szkuta, 2002	YES	Parke *et al.*, 2002 *Detached leaves susceptible*
Vaccinium spp.	Leaves		NPPO Ireland	YES	Parke *et al.*, 2002 *Detached leaves from resistant to susceptible depending on the species*
Veronica spicata	Leaves		APHIS		
***Viburnum* spp.**	Leaves and branches Trunk (PRA, APHIS)	YES	Werres *et al.*, 2001 Lane *et al.*, 2003 Husson *et al.*, 2007 RAPRA, COMTF, UK PRA 2003, ODA 2003…	YES	Parke *et al.*, 2002 UK PRA, 2003 V. tinus *leaves highly susceptible* UK PRA 2003, Inman *et al.*, 2002

					V. opulus *leaves resistant* Linderman *et al.*, 2006 *Leaves susceptible* Inman *et al.*, 2003 V. *spp. moderately susceptible*

4 Risk mapping

4.1 Choice of model

P. ramorum is regarded, in both the United States and Great Britain, as an invasive species that is far from having reached its potential distribution (Venette and Cohen, 2006; Kluza *et al.*, 2007; Linderman and Davis, 2007; Meentmeyer *et al.*, 2008; Spaulding and Rieske, 2011; Chadfield and Pautasso, 2012; Ireland *et al.*, 2013). Moreover, too little is known about its area of origin, although it has been suggested that it is indigenous to the mountains of the northern Indochina Peninsula where it has been identified (Sapa, Vietnam, IUFRO Workshop on *Phytophthora* in Forests and Natural Ecosystems, 2017). It is therefore unwise to use a distribution model with parameters fitted to the known presence of the species in the western United States or Europe (Guo *et al.*, 2005; Kluza *et al.*, 2007) to extrapolate the risk to another geographical area such as France.

Models based on knowledge of the effect of environmental factors on the oomycete seem more relevant. Two of these models have been used in a wide variety of situations in Europe and North America.

The first is based on the generic framework of CLIMEX (Venette and Cohen, 2006; Sundheim *et al.*, 2009; Ireland *et al.*, 2013). The latest version of this model parameterised by Ireland *et al.* (2013) provided rather pessimistic predictions for France, since the entire country was classified as highly favourable to *P. ramorum*. However, the ecoclimatic index used, with a relatively low threshold, seemed to correspond more to the establishment capacity of *P. ramorum* than to its ability to produce a major epidemic. It can be noted that the entire United Kingdom is also classified as very favourable.

The second model, developed and validated in California by Meentemeyer *et al.* (2004), has been used for Oregon and Europe (Vaclavik *et al.*, 2010; Sansford *et al.*, 2009). Its conclusions, integrated into the RAPRA project, mainly identified Brittany and south-west France as areas favourable to *P. ramorum* (Figure 12), in line with the predictions of Seidi *et al.* (2018) using another modelling approach. A few limited areas have a risk level equivalent to that calculated for south-west England, in the Ardennes and a small fringe in the Mediterranean area.

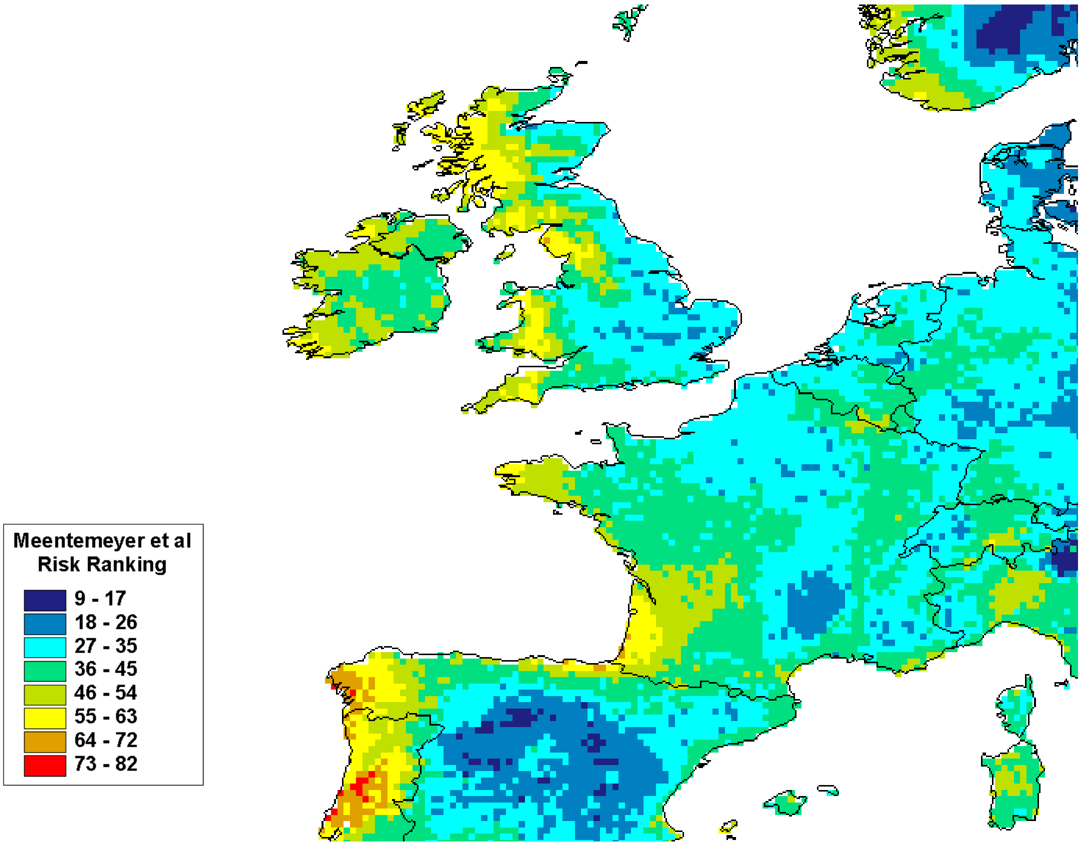


Figure 12: Map from the RAPRA report (2009) with a focus on France, showing the results from applying the Meentemeyer *et al.* (2004) model for the risk associated with *P. ramorum* as a function of climate

We opted to use this model thereafter because it provides a coherent framework for summarising the effect of climate and availability of competent hosts on the potential distribution of *P. ramorum*, which is not the case with the CLIMEX model. Competence had not been mapped within the framework of RAPRA. For the climate part, we believed it important to revisit the application of the Meentemeyer's model to Europe, and especially France, by examining in particular the sensitivity to the meteorological data used and any possible adaptations of the model related to local conditions.

4.2 Vegetation competence map for *P. ramorum*

One of the advantages of the model developed by Meentemeyer *et al.* (2004) is that it proposes a method for characterising the competence of vegetation, i.e. its ability to allow the oomycete to multiply, and then combining this information with information on the favourable nature of the climate.

Scores from 1 to 10 were assigned to the different woody species, based on the literature data summarised in the previous sections. The assigned score was directly related to the competence category defined in Table 8. As previously reported, shrub species systematically have a competence category at a level below that of comparable tree species in terms of inoculum production. This was also applied to the sapling stages of trees: score of 5 for *Larix*, 3 for sweet chestnut and holm oak, and 2 for *Q. cerris*, *Q. rubra*, black locust and ash when they are at seedling or shrub stage.

Table 8: Forest species competence score

Species	Latin name	Competence	Co. Score
Larch	*Larix kaempferi, L. eurolepis, L. decidua*	High	10*
Sweet chestnut	*Castanea sativa*	Moderate to high	5*
Holm oak	*Quercus ilex*	Moderate to high	5*
Rhododendron	*Rhododendron ponticum*	Moderate to high	5
Strawberry tree	*Arbutus unedo*	Moderate to high	5
Common ash	*Fraxinus excelsior*	Moderate	3*
Black locust (false acacia)	*Robinia pseudoacacia*	Moderate	3*
Oak	*Quercus cerris, Q. rubra*	Moderate	3*
Italian buckthorn	*Rhamnus alaternus*	Low to moderate	2
Viburnum	*Viburnum tinus*	Low to moderate	2
Heather	*Calluna vulgaris*	Low to moderate	2
Lilac	*Syringa vulgaris*	Low to moderate	2
Blueberry	*Vaccinium myrtillus*	Low to moderate	2

*Reduced score if in the understory

A score was then assigned to the plant community present in all plots rated by the IFN from 2005 to 2016 (approximately 77,000 plots). The plot score was calculated as the sum of the scores of the species present weighted by the extent of their presence. This was assessed according to the proportion of basal area represented by the species for trees, and according to the Braun-Blanquet abundance-dominance coefficient of the species for understory woody species (0.025, 0.15, 0.375, 0.625 and 0.825 for coefficients from 1 to 5). The presence of tree species in the understory (seedling to shrub stage) was taken into account as explained above.

The competence score of a plot was therefore:

$Co_i = (100/15) \times (\Sigma_j (Co_j \times Pst_{ij}) + \Sigma_k (Co_k \times AD_{ik}))$

Where Co_j and Co_k are the competence scores of trees j and understory woody plants k, Pst_{ij} is the proportion of species j in the basal area of plot i, and AD_{ik} is the abundance-dominance score of the understory woody species k in plot i. The Co_i index was scaled to vary from 0 to 100 (the value of 15 is the maximum vegetation competence score attributable to a plot). The plot scores were then analysed by a hierarchical Bayesian model with spatial dependence to estimate a smoothed spatial effect (model using INLA with a Beta distribution). Only sampling points where forest was present were taken into account. The result therefore represents only the mean competence of forest stands for *P. ramorum*.

Figure 13a shows the resulting competence map. The areas for which mean competence of forest stands is high, are especially in the Southern Alps (larch forests) and, to a lesser extent, in Languedoc and Corsica (dense areas of holm oaks, sweet chestnut and/or strawberry trees).

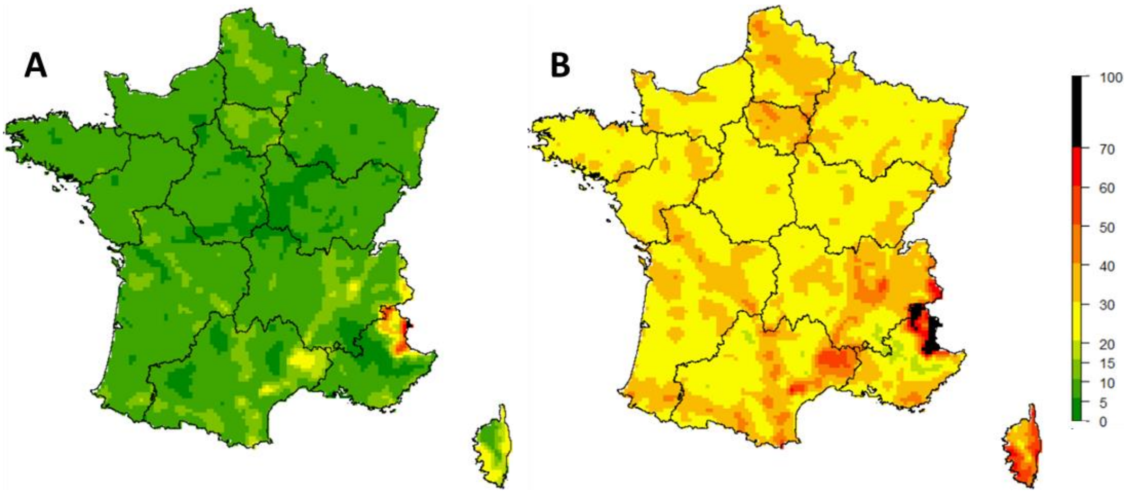


Figure 13: Competence of forest stand vegetation (Co_i) for *P. ramorum*. A. mean value, B. 95% quantile. The map was obtained after smoothing by analysis with a hierarchical Bayesian spatial model and the 95% quantile was calculated according to the estimated parameters of the Beta distribution (mean and precision).

It may seem surprising that the vegetation of Finistère was characterised as having relatively low competence when this is where an epidemic has developed in the wild. This map only represents an average situation and therefore only provides information on the overall level of risk in Finistère and elsewhere in France. It would be a misinterpretation to deduce from this that there are no highly competent stands in Brittany and that no epidemic can develop there. The presence of stands at risk of an outbreak is best represented by the 95% quantile map of the competence score, which provides information on the 5% of local stands with greatest competence. It should be noted that Finistère remains a region with a relatively limited risk on the basis of this criterion (Figure 13b). For example, within a 30 km radius of the affected larch stands in the Sizun outbreak, sweet chestnut is present in the overstory of 21% of the IFN plots and in the understory of 36% of them. Other plants occurring with a significant level of competence are blueberry (19%), heather (13%), ash (5%), larch (3%) and rhododendron (2%). It can be seen that *R. ponticum* is relatively rare in the forest and has little influence on the calculated competence. However, it should be noted that this competence map only represents forest vegetation and does not integrate the local extent of forest stands or the competence of non-forest vegetation (e.g. hedges, parks and gardens). In particular, Finistère is one of the few areas where *R. ponticum* occurs more markedly in the wild, where it is regarded as an invasive alien species (Figure 14). Other woody species with high competence such as sweet chestnut or ash in hedges could also be underestimated in Figure 14 because they are potentially abundant in non-forest vegetation. It is thus possible that there have been particularly abundant relays between the forest and rhododendron grown in parks, gardens or nurseries in Finistère.

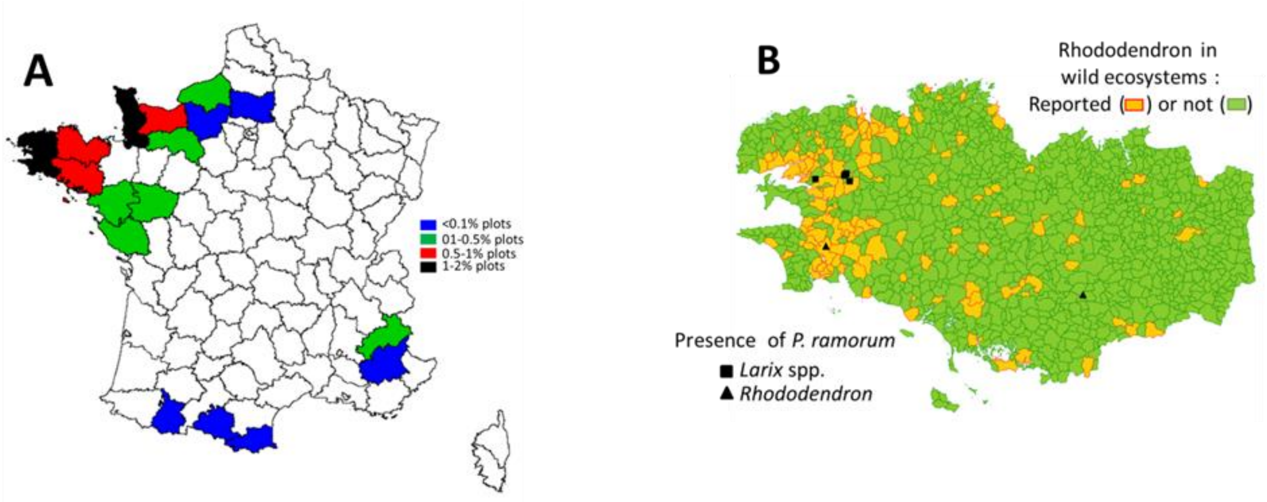
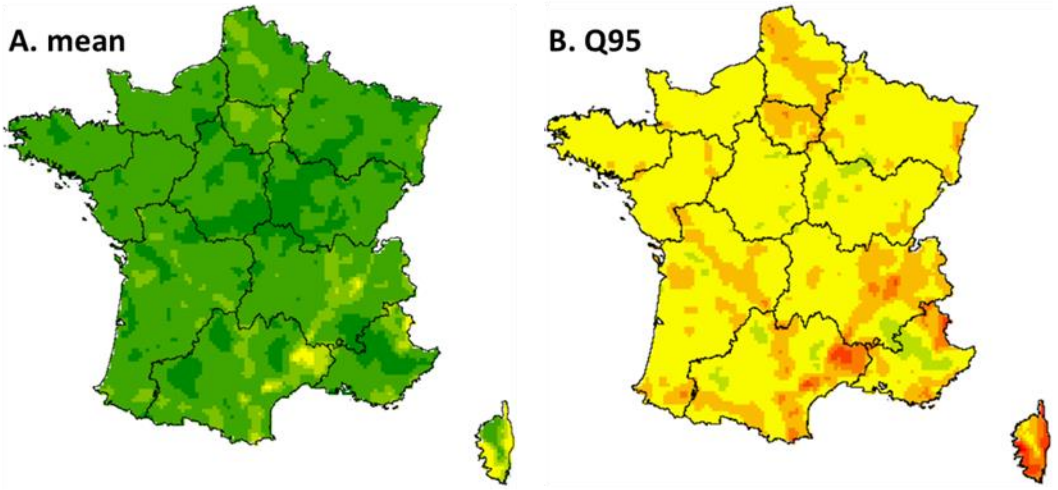


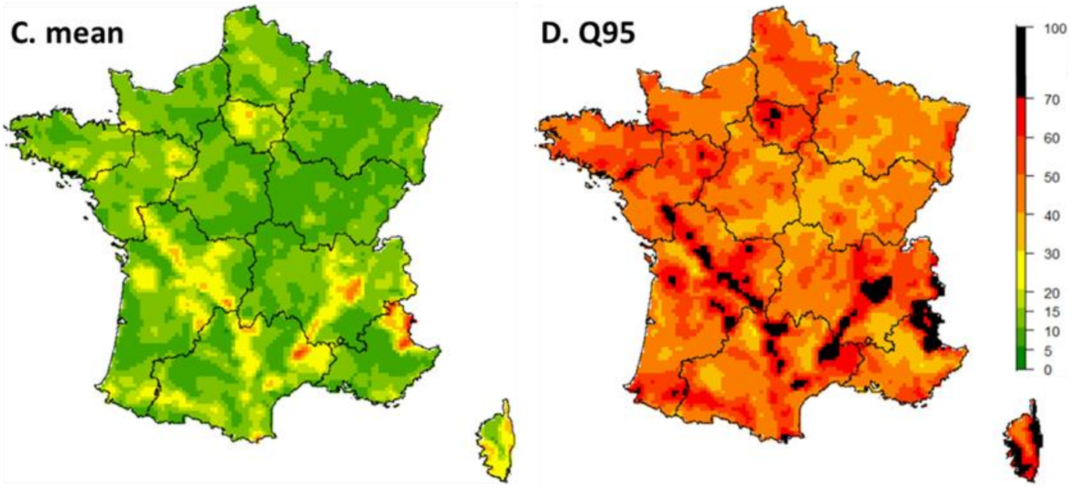
Figure 14: Map of the presence of rhododendron in the wild. A. In France, according to data from the National Forestry Inventory (2005-16), B. In Brittany, according to data from the National Botanical Conservatory of Brest. The presence of *P. ramorum* reported by the DSF is indicated on this map.

A sensitivity analysis was carried out to measure the impact of the high uncertainty on knowledge of the competence of the woody species found in France. Maps were produced by modifying the scores for European larch (Co score of 5 instead of 10 for *L. decidua*), sweet chestnut (score of 10 instead of 5) or honeysuckle (score of 2 instead of 0). This third map was produced to take account of the fact that there is a lack of knowledge on many of the woody species in the understory. Honeysuckle (*Lonicera periclymenum*) was chosen because it has a widespread presence (in one third of IFN plots in France and 50% of plots in Brittany) and, although its leaves are not highly susceptible, it could enable *P. ramorum* sporulation (Sansford *et al.,* 2009). This analysis explored what would happen if a common understory woody species played a significant role in transmission of the disease. Not surprisingly, if the *L. decidua* score is reduced, vegetation in the Southern Alps appears to be far less favourable to the development of *P. ramorum* (Figure 15 a and b). On the other hand, if sweet chestnut had a higher competence than previously considered, this would have major consequences (Fig 15 c and d). A band of forest vegetation with high competence then appears from southern Brittany to the Montagne Noire, and then from the southern Cévennes to western Isère, corresponding to a significant presence of sweet chestnut. This represents a potential corridor of spread for *P. ramorum*. Lastly, if a common understory woody species such as honeysuckle had significant competence, this would promote the overall spread of the epidemic, with competence increased quite markedly, even if the location of the areas most at risk would be only slightly modified (Figure 15 e and f).

L. decidua= 5



C. sativa= 5



L. periclymenum = 2

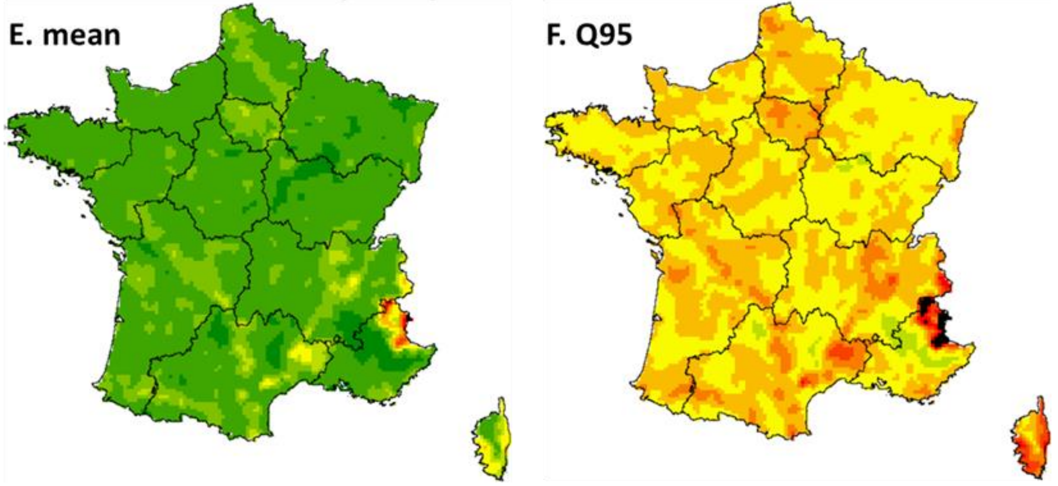


Figure 15: Analysis of the sensitivity of the forest stand vegetation competence score for *P. ramorum* to the scores for certain species. Change in scores compared to the map shown in Figure 12 for *L decidua* (A and B, Co=5), *C. sativa* (C and D, Co=10) and *L. periclymenum* (E and F, Co=2). The 95% quantile was calculated according to the estimated parameters of the Beta distribution (mean and precision).

4.3 Climate mapping: adaptation of the model of Meentmeyer *et al.* (2004)

4.3.1 Description of the model

The model developed by Meentemeyer *et al.* (2004) is based on scores representing the more or less favourable nature of the climate for *P. ramorum* and the local availability of competent hosts, to an equal degree.

The climate part consists of a calculation of monthly scores that reflect the mean daily maximum and minimum temperatures, the mean relative humidity, and the sum of precipitation according to the scale shown in Table 9. These scores (Sc_i) are averaged to determine the favourable nature of month i with a relative weight that depends on the climatic parameter (2 for precipitation sP_i and the mean daily maximum temperatures mTX_i, 1 for relative air humidity mHR_i and the mean daily minimum temperatures mTN_i):

$Sc_i = (100/26) \times (2\ sP_i + 2\ mTX_i + mHR_i + mTN_i)$

These scores were calculated for the months of December to May, which correspond to the sporulation period of *P. ramorum* in California, and the final score for a given site was calculated as the mean of the monthly scores scaled to vary between 0 and 100 (26 is the maximum value reached by the quantity $2\ sP_i + 2\ mTX_i + mHR_i + mTN_i$).

In the RAPRA project (Sansford *et al.*, 2009), the climate data used to calculate the scores came from the Climate Research Unit (CRU) using the European database with a grid of 10' in longitude and latitude and the period from 1961 to 1990 (http://www.cru.uea.ac.uk/). This database does not include the relative humidity of the air and this parameter was therefore omitted from the score:

$Sc_i = (100/21) \times (2\ sP_i + 2\ mTX_i + mTN_i)$
(21 is the maximum value reached by the quantity $2\ sP_i + 2\ mTX_i + mTN_i$)

Table 9: Scores used for the climate variables in the Meentemeyer *et al.* (2004) model

Score	Precipitation[a] (mm)	Maximum temperature[b] (°C)	Relative air humidity[c] (%)	Minimum temperature[b] (°C)
5	>125	18-22	>80	-
4	100-125	17-18 or 22-23	75-80	-
3	75-100	16-17 or 23-24	70-75	-
2	50-75	15-16 or 24-25	65-70	-
1	25-50	14-15 or 25-26	60-65	>0
0	< 25	<14 or >26	< 60	< 0

[a] Monthly totals, [b] Mean daily maximum-minimums, [c] Monthly mean

The climate data used for our work were those of the CRU (1961-2000, 10' grid on Europe) and the Chelsa database (http://chelsa-climate.org), available at high resolution (30'', i.e. about 1 km) on a global scale for mean monthly temperatures (daily maximum and minimum temperatures) and precipitation for the period 1979-2013. As relative air humidity values are not available from the Chelsa database, the calculation was performed as for the CRU database data. Lastly, for France, we used Safran data (1985-2015 period), available as daily data on a coarser 8 x 8 km grid but with relative air humidity data available.

4.3.2 Different climates where *P. ramorum* is present in natural ecosystems

Western United States

The Meentemeyer *et al.* (2004) model was used in California and Oregon to determine the potential area of presence of *P. ramorum*. This model gave satisfactory results in both cases, with the locations where *P. ramorum* is effectively present correctly being assigned as favourable to highly favourable to its development. In addition, it was possible to compare the predictions made in California in 2004 to the development of the disease over the next 10 to 15 years. This model assessment showed that the probability of subsequent invasion by *P. ramorum* was predicted to an acceptable degree (Meentemeyer *et al.*, 2008). The calculated monthly score indicated a very marked seasonal trend in the Californian sites shown in Figure 16, with winter months from October to May favourable to the disease (mild and damp Mediterranean winter) while summer months being too dry and too hot and therefore far less favourable. Several authors showed that summer stress is high, with cessation of sporulation, and survival in infected leaves of *Umbellularia californica* decreasing significantly during the season (Davidson *et al*., 2008; Fichtner *et al.*, 2007; Fichtner *et al.*, 2009). This very unfavourable period does not prevent the epidemic from restarting in the autumn.

Europe

In Europe, *P. ramorum* has been found in the wild mainly on the western side of Great Britain and in parks and gardens in various countries (particularly Great Britain, the Netherlands and Norway). The climate in European areas where *P. ramorum* causes epidemics in the wild is very different from that in the western United States. Indeed, Figure 16b shows that the periods favourable to multiplication of the oomycete, according to the scores calculated with Meentemeyer's model, are during summer and early autumn with sufficiently warm and damp conditions, while winter is too cool to be favourable, either on the west coast of Great Britain or in Finistère. Observation data on the *P. ramorum* sporulation period in Great Britain are fragmentary, but support this finding (spring to autumn sporulation with a peak around October and November, J. Webber, personal communication). However, this point remains insufficiently documented.

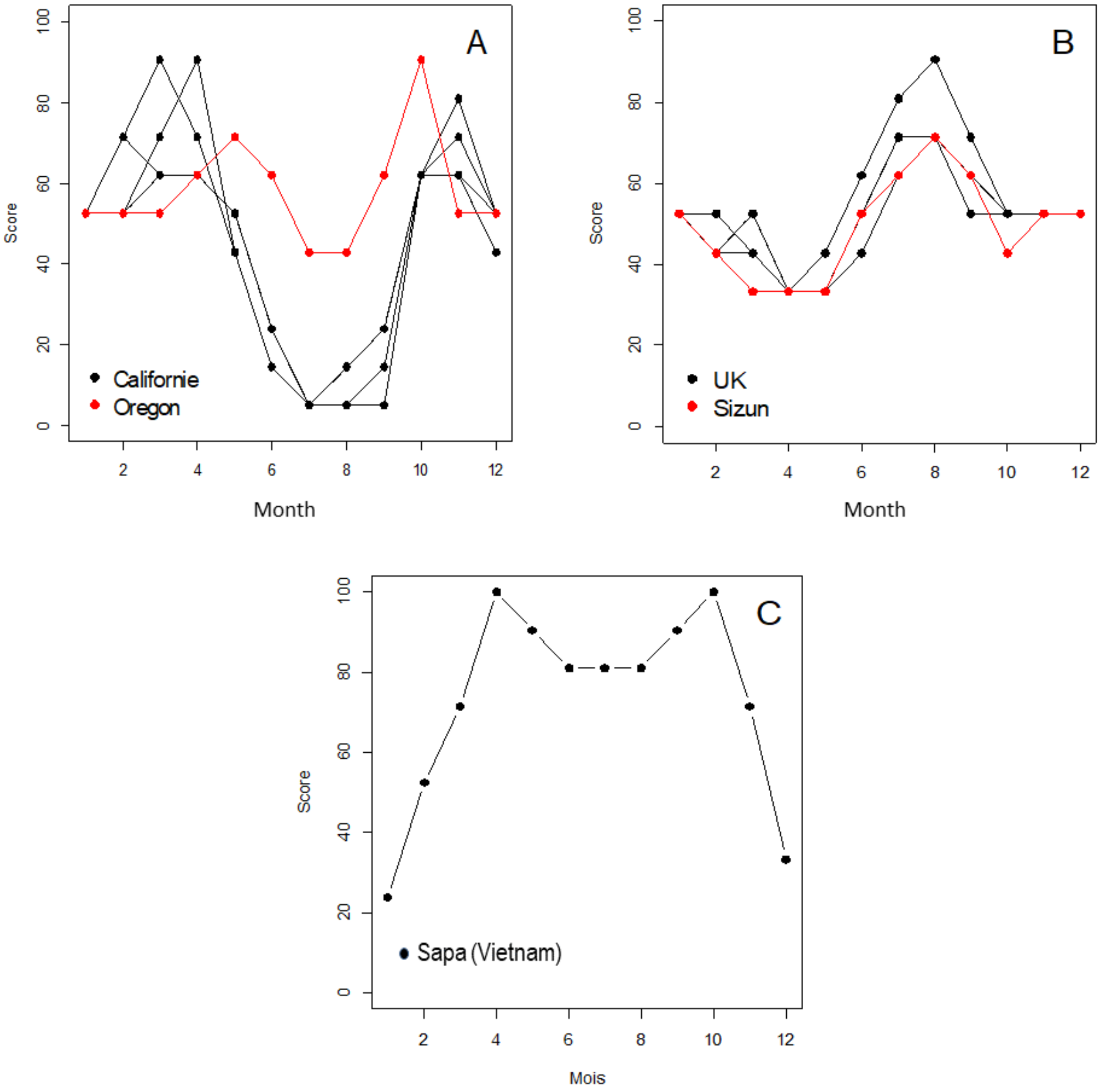


Figure 16: Monthly scores from the Meentemeyer *et al.* (2004) model using Chelsa climate data (1979-2013) for three geographical areas. A. North-west America: three sites in California and one in Oregon, B. Western Europe: three sites in Great Britain (southern Scotland, Wales and Cornwall) and one site in France (Sizun, Finistère = outbreak on larch), C. Vietnam: Sapa, the locality where *P. ramorum* was detected.

In the RAPRA project, Meentemeyer's model was applied without adaptation to the climate of Atlantic Europe, with the score being calculated over the period from December to May, which seems irrelevant in view of the results in Figure 16. However, Figure 17 shows that taking into account the period from December to May or the whole year ultimately makes little difference to the risk mapping, even if taking the growing season into account logically leads to higher risk scores overall, since it includes the most favourable period for *P. ramorum*. The order of magnitude of the highest scores (60-65) corresponds to the scores obtained with the same data and calculations for the areas in California and Oregon where SOD is mentioned (result not shown). The areas where *P. ramorum* outbreaks are present generally correspond closely to the areas identified as favourable for the disease (Fig 17c).

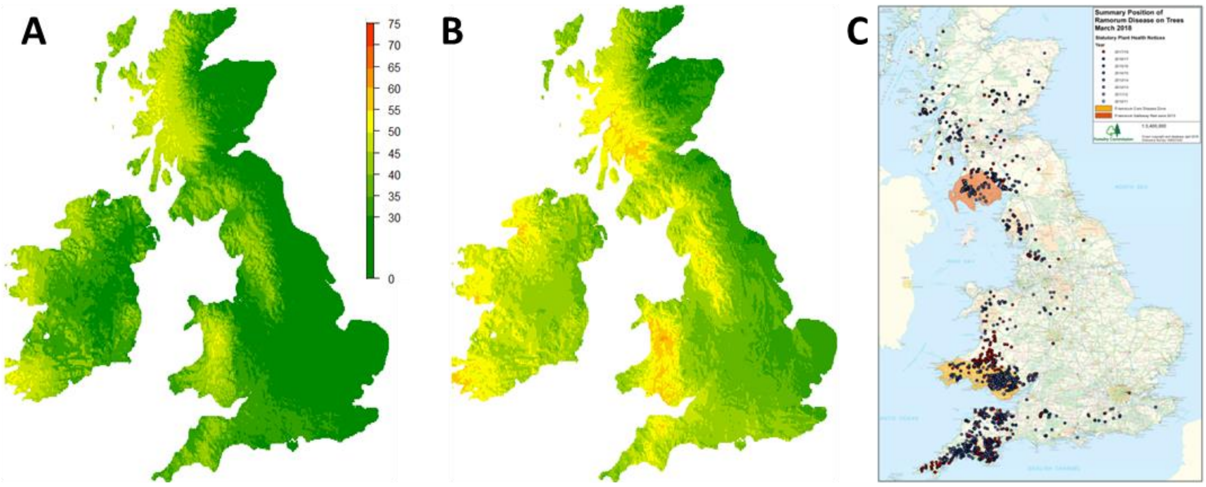


Figure 17: Risk map of *P. ramorum* as a function of climate according to the Meentemeyer *et al.* (2004) model – without relative humidity – for Great Britain (Chelsa Climate Data, 1979-2013). A. Climatic data for the months of December to May. B. For the entire year. C. Location of outbreaks of *P. ramorum* on larch in Great Britain in 2018 (the light and dark orange represent areas where strict quarantine is no longer applied because *P. ramorum* is too widespread).

There is no strong constraint on survival in Britain during the unfavourable period (here winter). It has been shown that *P. ramorum* can withstand the periods of moderate freezing temperatures that characterise Europe's maritime climate. Some data are available on its survival at negative temperatures under controlled conditions. *P. ramorum* chlamydospores survived well after one to seven days of exposure to temperatures of 0 to -2°C *in vitro*, but they did not survive after one day at -10°C (Tooley *et al.*, 2008; Turner *et al.*, 2005). The inoculum present in infected leaf tissue persists much better, since *P. ramorum* was re-isolated from 100% of rhododendron leaf discs exposed for seven days in soil to -10°C (Tooley *et al.*, 2008). *P. ramorum* inoculum in rhododendron or lilac leaves had a survival rate of about 50% after exposure in litter on the soil surface to 4 months of British winter conditions (winter 2003-04, relatively mild, but with a minimum air temperature of -9°C, Turner *et al.*, 2005). Lastly, it has been shown that *P. ramorum* can become established in semi-natural conditions on the coasts of southern Norway (Sundheim *et al.*, 2009, park and garden situation), under conditions where the average minimum temperature in the coldest month is around -1 to -3°C (CHELSA data, result not shown). Based on all these data, Ireland *et al*. (2013) only integrated a deleterious effect of low temperatures on the survival of *P. ramorum* with a very low threshold (-8°C mean weekly temperature). However, it should be noted that the CLIMEX model developed by Ireland *et al.* (2013) is not designed to describe the epidemic risk, but the probability of naturalised populations of *P. ramorum* becoming established, which is quite different.

South-east Asia

In south-east Asia, the presence of *P. ramorum* has been confirmed in Sapa, in the mountains of northern Vietnam where it has been suggested to be indigenous (Webber, 2017, https://www.forestresearch.gov.uk/news/finding-phytophthora-ramorum-in-the-natural-environment-of-north-vietnam/). A brief look at the climate of this region therefore seemed useful. Climatic conditions are very favourable to *P. ramorum* from March to November, with peaks in spring and autumn (Figure 16c). If a closer look is taken at the components of the score, the share of rainfall remains at 5 between April and October while the share of daily maximum temperature oscillates between 3 and 5 during this period. The unfavourable period is short, from December to February, with rainfall and daily maximum temperature scores of 1 to 2. There are no periods with temperatures below 0°C on a sustainable basis: the mean daily minimum temperature of the coldest month always remains above 0°C.

4.3.3 Use of the model for France

The previous analysis illustrates the ability of *P. ramorum* to develop in very different climates: tropical mountains with high precipitation and a hot season with moderate temperatures, Mediterranean climate with mild damp winters and very dry hot summers, or maritime zones with mild winters and cool damp summers. The model developed by Meentemeyer *et al.* (2004) gives satisfactory results in these three very contrasting climates. On the other hand, it does not seem appropriate to use it without adapting it, as was the case in the RAPRA project, since the periods favourable to *P. ramorum* development are not the same in the climates of the western United States and Brittany. The period must therefore be adapted. The decision was made to take the whole year, because France is characterised by very contrasting climates (oceanic, semi-continental, Mediterranean) and the choice of a restricted period such as from May to November would be difficult to justify for all these climates.

A potential limitation of Meentemeyer's model is the lack of explicit consideration of survival constraints. The unfavourable summer period is not included in the model, originally designed for the Californian climate. The underlying assumption is that there is always enough primary inoculum left at the start of the favourable season to allow the pathogen to cause an epidemic if conditions during that season are favourable, due to its very high asexual multiplication. This is a common hypothesis in plant pathology, but may be unrealistic under marginal conditions (climatic area boundary, unfavourable site, low density of competent hosts). Constraints related to the cold, to hot temperatures and water stress, are on the other hand integrated into the CLIMEX model developed by Ireland *et al*. (2013) for *P. ramorum* worldwide. According to the results of these authors, these constraints should be too weak in France to prevent the establishment of naturalised populations of *P. ramorum* (Figure S1, S4, S5 in Ireland *et al*., 2013). However, as already pointed out, it is still possible that some of these constraints could limit the extent of the induced epidemic. We did not test adaptation of the model for the summer survival constraint in hot dry summer conditions because Meentemeyer's model works well for the Californian Mediterranean climate (80% of the observed disease reports concerned areas predicted to have a moderate to very high risk).

However, it seemed interesting to test the model's sensitivity to a survival constraint during winter frosts. To do this, we took inspiration from what was done in the CLIMEX model: the mean annual score was multiplied by a survival coefficient that depended on the mean daily minimum temperatures of the coldest month: 1 for values above -1°C, 0.8 from -1 to -2.5°C, 0.6 from -2.5 to -5°C, 0.4 from -5 to -7.5°C and 0.2 below -7.5°C. This is an upper-bound hypothesis in which negative temperatures have a much greater effect on the winter survival of *P. ramorum* than that considered by Ireland *et al.* (2013). Figure 18 shows that this could have major effects in mountainous areas.

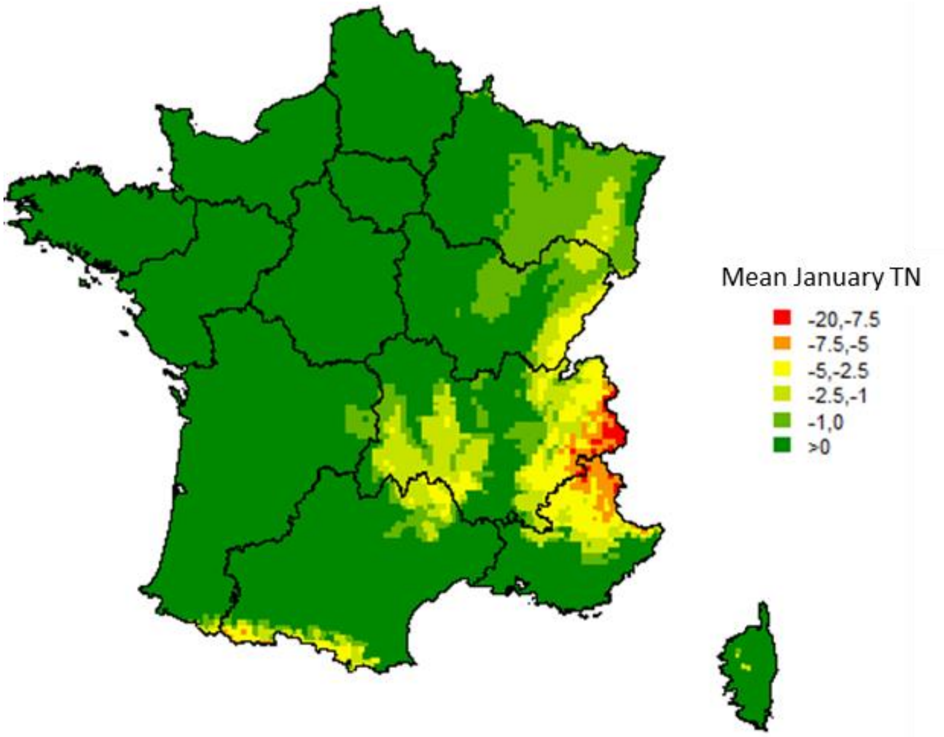


Figure 18: Mean minimum January temperatures (Safran climate data, 1985-2016)

4.3.4 Results

Comparison of databases and assessment periods

Figure 19 shows the outputs from the Meentemeyer *et al.* (2004) model for three sets of weather data covering different periods (1960-90, 1979-2013 or 1985-2006) and initially excluding relative air humidity, which is only available for SAFRAN data. The map in Figure 19a shows the output that was available through the RAPRA project, except for scale. Indeed, in this project the index was scaled to vary between the minimum and maximum values observed in Europe whereas we scaled it to have a theoretical index from 0 to 100, regardless of the values observed for Europe; this was done to facilitate comparison between the maps. Figure 19a only identifies a *P. ramorum* epidemic risk on the Atlantic coast, Aquitaine, Limousin and Brittany. Taking the entire year into account markedly changes the risk assessment (Fig 19d). Indeed, in addition to the fact that the risk in Limousin and Brittany is revised upwards, new high-risk areas have emerged (Ardennes, Jura and Pyrenees). The consideration of other climatic data over a different period (SAFRAN, 1985-2016, CHELSA, 1979-2013) also considerably modifies the risk assessment, with the mountain ranges of eastern France becoming more favourable to *P. ramorum*, and the emergence of a marked risk on the ridge of the Cévennes and on the Montagne Noire (Figures 19e and 19f). Further analysis revealed that the difference does not come from the period, but from an underestimation of rainfall over French mountain ranges in the CRU dataset (result not shown). On the other hand, the outputs from CHELSA and SAFRAN data are highly consistent.

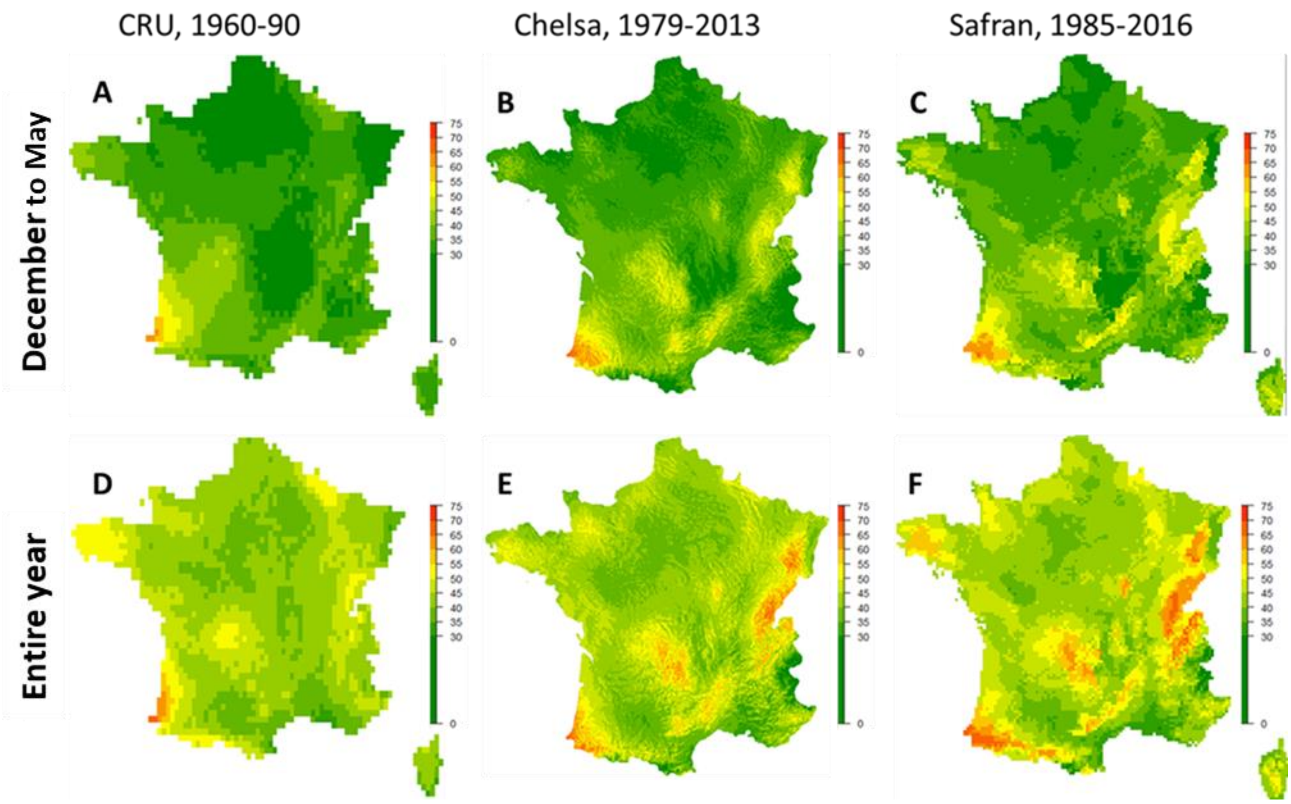


Figure 19: Risk map of *P. ramorum* as a function of climate (Sc_i risk scores) according to the Meentemeyer *et al.* (2004) model for France. The model results are presented using several climate datasets (A and D, CRU Safran, 1960-90, B and E, CHELSA, 1979-2013, C and F, SAFRAN, 1979-2013) and two different periods for the calculation (A, B and C, months of December to May, D, E and F, the entire year). To allow comparison, calculations were performed for the three datasets excluding relative air humidity.

Final result of risk scores

The mapping of areas that are climatically favourable to *P. ramorum* was ultimately carried out using SAFRAN data for the period 1985-2016 because of the availability of air humidity data (Figure 20). Taking relative air humidity into account in the score calculation did not significantly change the ranking of the zones, but increased the score over almost the entire country. However, the Southern Alps and the Mediterranean area remain at an unfavourable level. What is revealed compared to the map presented in the RAPRA project using the same model (i.e. Meentemeyer's, but without adaptation of the sporulation period and with partial and inaccurate climatic data – see above) is that a significant risk is identified in all mountainous areas, particularly in eastern France (Vosges, Jura and northern Alps), in the Morvan and on the Montagne Noire and Cévennes, as well as on the entire Channel coast, especially in the Cotentin. The model is moderately sensitive to the inclusion of a strong winter survival constraint (Figure 20c). The risk may then be reduced in the Alps, the Jura and southern Auvergne. This points to a lack of knowledge on the effect of winter survival that will be difficult to rectify if *P. ramorum* does not extend to areas with more severe winters.

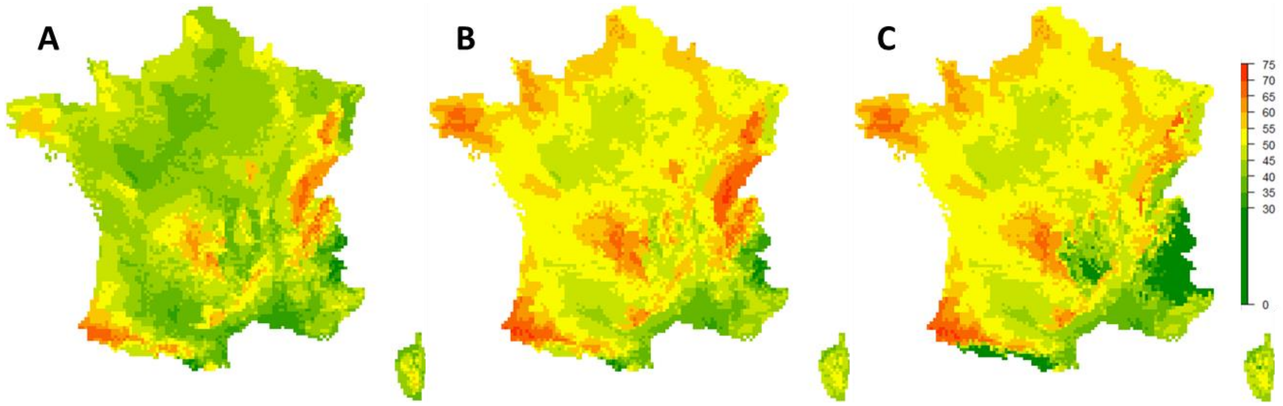


Figure 20: Mapping of the favourable nature of the climate to *P. ramorum* according to the adapted Meentemeyer model using SAFRAN data (1985-2016). A. Excluding relative air humidity from the score calculation (map F in the previous figure), B. Including relative air humidity, C. Including relative air humidity and a winter survival constraint.

Lastly, Figure 21 shows the risk value taking into account both the competence of forest vegetation and climate. This index is calculated as the average of the scores for vegetation competence (Sc_i) and climate suitability to *P. ramorum* (Co_i, Figure 20b). The alpine larch zone, with its particularly competent vegetation, has the highest values, unless the competence score of *L. decidua* is reduced, despite a rather unfavourable climate. On the other hand, the Jura has a fairly high risk score with a very favourable climate but only slightly competent vegetation. Beyond that, the areas in Brittany, Limousin, Cévennes, Montagne Noire, the Pyrenean foothills (particularly the western side of the Pyrenées), eastern Isère and Corsica are those where the risk is greatest, if the competence score for sweet chestnut is raised.

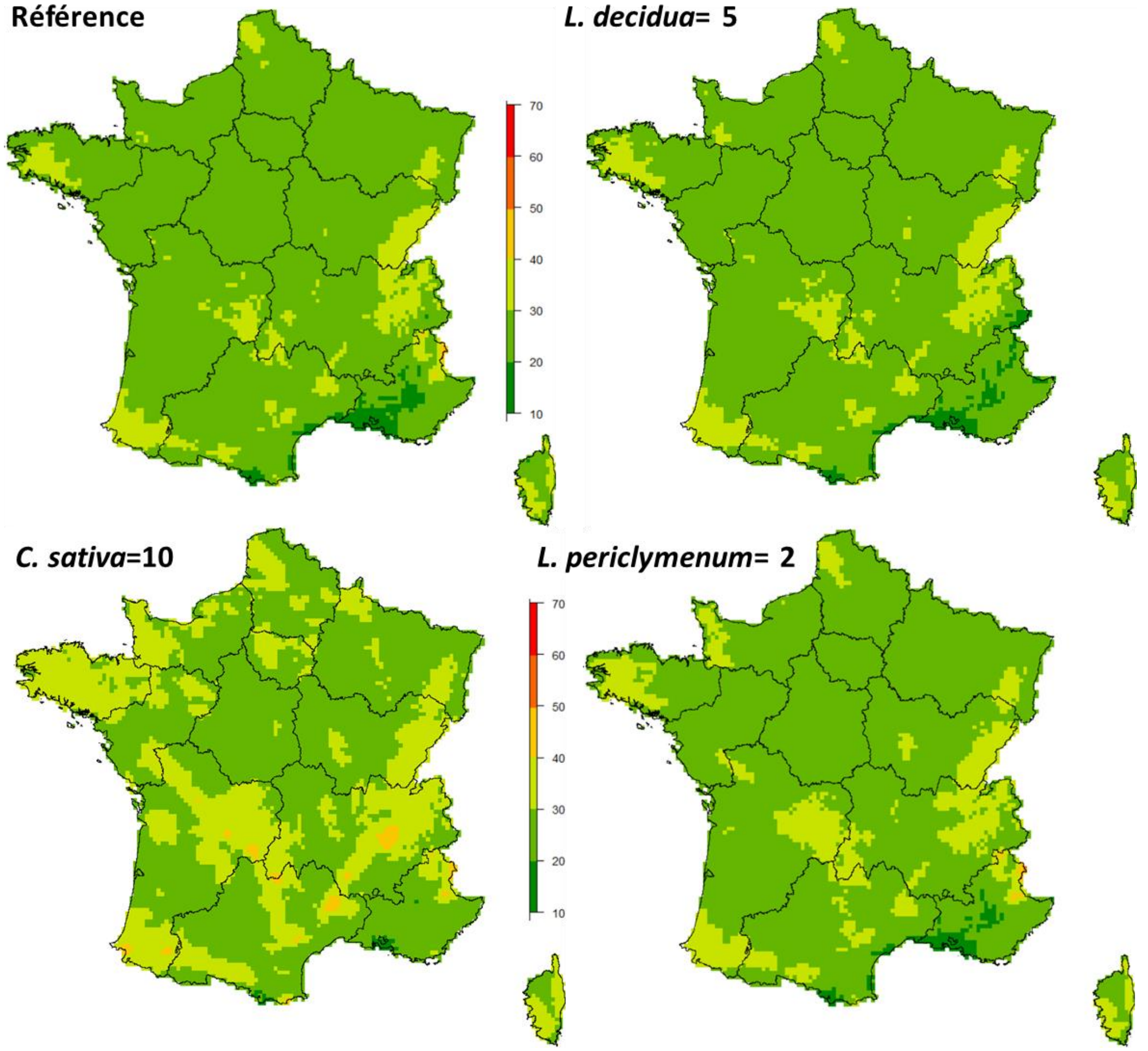


Figure 21: Overall risk (climate + vegetation competence) for *P. ramorum* according to the Meentemeyer *et al.* (2004) model over the entire year (SAFRAN data for 1985-2016 and forest vegetation competence according to IFN data for 2005-16). For the reference map, the competence scores used are given in Table 9. The other three maps were produced by modifying the competence score for the species indicated.

This is particularly clear when maps constructed with the 95% quantile of competence are considered (Figure 22).

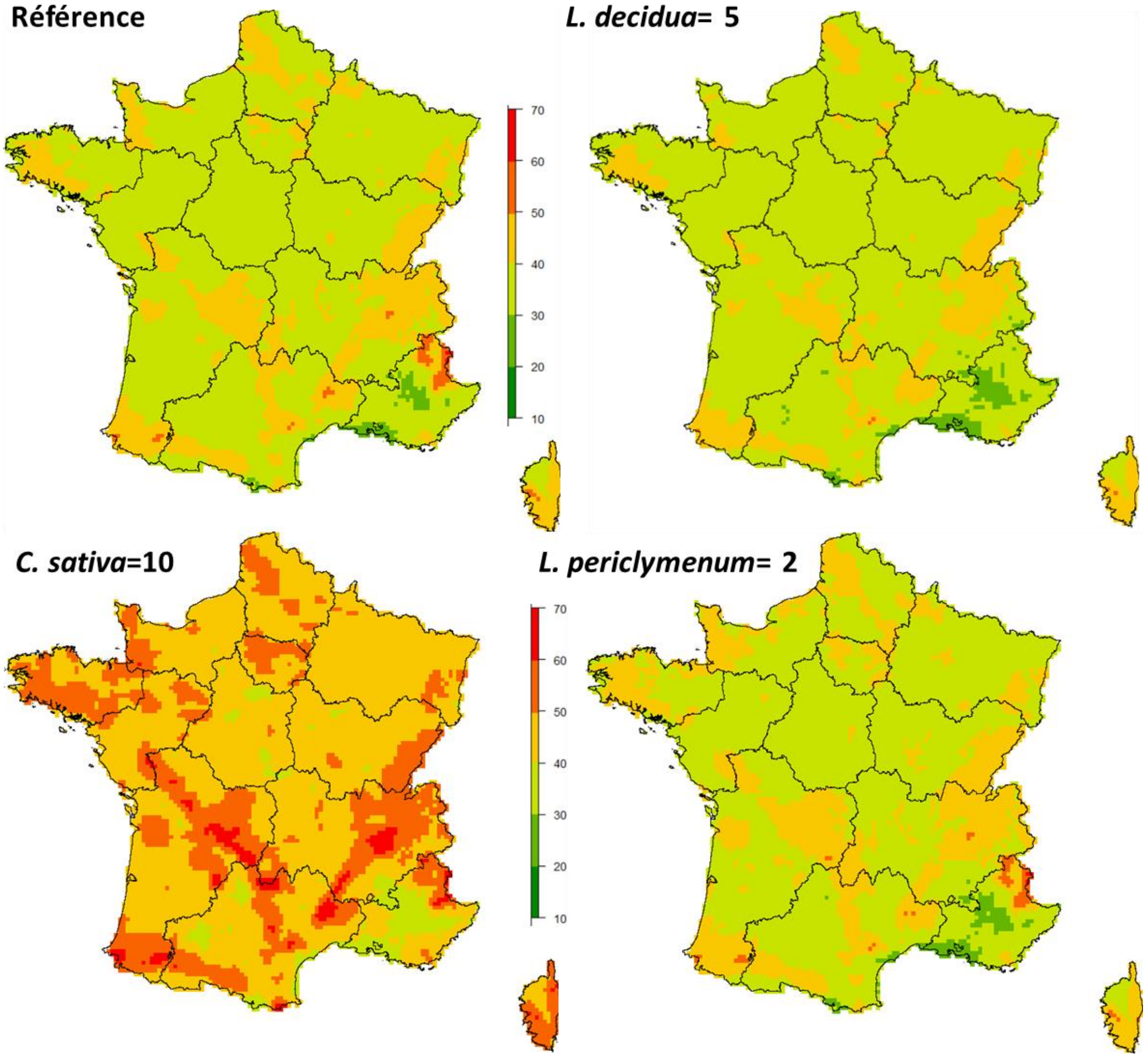


Figure 22: Overall risk (climate + vegetation competence) for *P. ramorum* according to the Meentemeyer *et al.* (2004) model over the entire year using the 95% quantile map of forest vegetation competence (SAFRAN data for 1985-2016, Figure 20b, and forest vegetation competence according to IFN data for 2005-16). For the reference map, the competence scores used are given in Table 9. The other three maps were produced by modifying the competence score for the species indicated.

The location of tree species identified as having significant competence on the climate risk map (Figure 20b) helps better appreciate what is at stake (Figure 23 and 24). It can be seen that natural stands of larch (alpine larch forests) and holm oak are predominantly located in low-risk areas, in both the Alps and the Mediterranean area. However, the areas where larch is currently planted the most (Limousin or Montagne Noire, for example) are often areas with a climate favourable to *P. ramorum*. For ash, its presence is fairly widespread throughout the country, and especially in the north and north-east, and it will have a significant presence in all areas with a climate favourable to *P. ramorum*. Lastly, sweet chestnut is the host whose distribution is most in line with the climatic envelope of *P. ramorum* (with the exception of the stands in the Centre-West and Dordogne). This match between sweet chestnut distribution and the favourable climate for *P. ramorum* is all the more worrying as symptoms on sweet chestnut independent of inoculum sources from larch are currently being reported in Great Britain (Webber 2017).

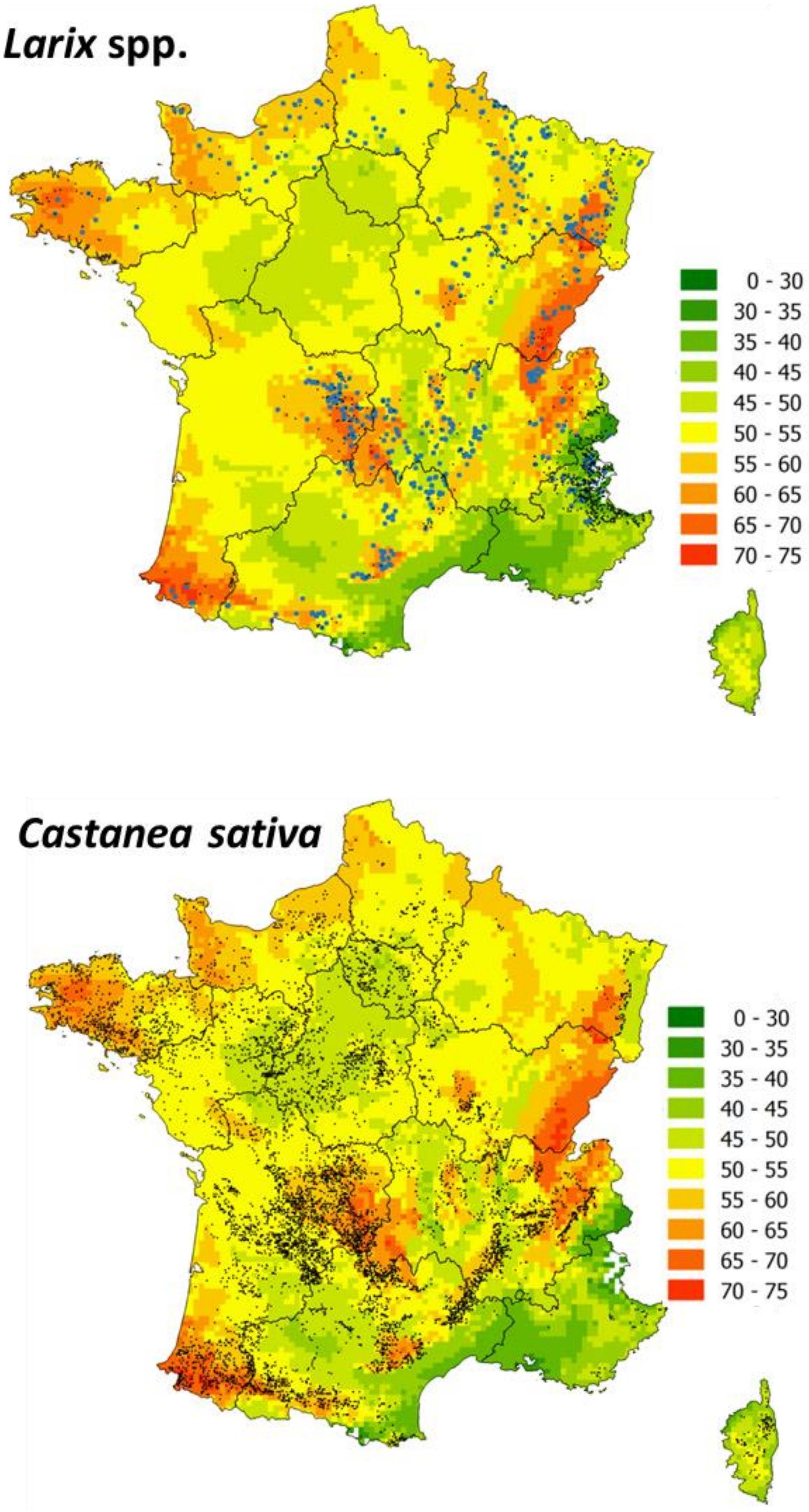


Figure 23: Location of *Larix* spp. and *Castanea sativa* (black dots = IFN data, 2005-2016) on the climate risk map obtained with the Meetemeyer *et al.* (2004) model over the entire year using SAFRAN data (1985-2016, Figure 19b). The blue squares on the *Larix* spp. map represent the locations of larch plots in the DSF's "plantation" surveys (2006-17).

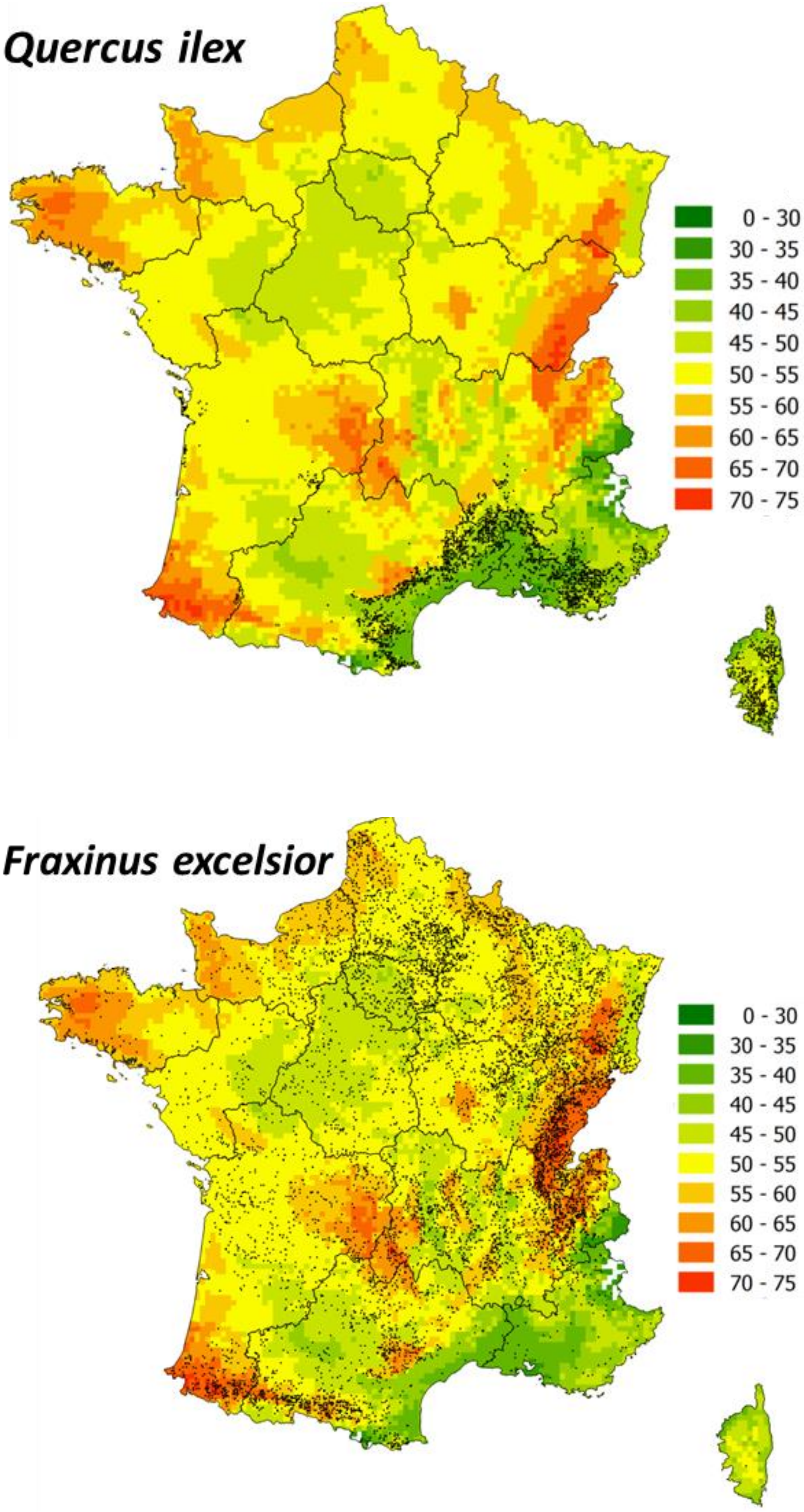


Figure 24: Location of *Quercus ilex* and *Fraxinus excelsior* (black dots = IFN data, 2005-2016) on the climate risk map obtained with the Meetemeyer *et al.* (2004) model over the entire year using SAFRAN data (1985-2016, Figure 19b)

5 Anthropogenic factors (excluding the effect of climate change) favouring the establishment and spread of *Phytophthora ramorum*

The role of ornamental plant trade, particularly through **nurseries and garden centres**, in the introduction and establishment of *P. ramorum* in the USA and Europe has been demonstrated by several epidemiological or genetic studies (Goss *et al.*, 2009; Grünwald *et al*., 2012; Mascheretti *et al*., 2008; Prospero *et al*., 2009; Croucher *et al*., 2013). Nurseries provide a favourable environment for the development of *Phytophthora* in general and *P. ramorum* in particular, as these organisms can persist, multiply and disperse in potting media or irrigation water (Parke and Lewis, 2007; Tjosvold *et al*., 2009; Fitchner *et al*., 2011). *P. ramorum* can remain viable in growing substrate for up to 33 months (Vercauteren *et al*., 2012). It can be spread by plants in many ways: latent or non-latent infections of leaves, stems or buds, and root or fruit infections (Denman *et al*., 2009; Migliorini *et al*., 2015). Due to its host range encompassing a large number of ornamental and forest species, *P. ramorum* can therefore be spread over long distances in diverse and varied plant material, and exchanged between different continents, countries or regions. The recent discovery of the EU2 lineage (Van Poucke *et al*., 2012) shows that these risks of introduction still prevail despite quarantine measures taken in Europe and the United States.

A list of regulated species has been drawn up by the USDA (https://www.aphis.usda.gov/plant_health/plant_pest_info/pram/downloads/pdf_files/usdaprlist.pdf); this list was largely used to draw up the list of plants requiring a European Plant Passport (EPP).

P. ramorum has thus been the subject of quite a number of interceptions during intra-EU checks, especially for plants (most often rhododendron or viburnum) exported from the Netherlands (EFSA, 2011). EPPO data show that interceptions have continued to be notified ("notifications of non-compliance") in recent years, for example 16 in 2016, including one from France (on camellia, to the United Kingdom), five from the Netherlands and seven from Belgium. Transfer of *P. ramorum* on infected plants exported to Japan from Europe has also been reported (Sakoda *et al*., 2017).

The DGAL (French Ministry of Agriculture) provided us with data on the detection of *P. ramorum* following visual inspections carried out since 2004 in nurseries (90% of all inspections) or garden centres, parks and gardens, or forests (targeted on *P. ramorum*) in France (data on cases reported at EU level).

The number of detections peaked in 2007 and 2008, with about 2% of inspections revealing positive cases in nurseries and garden centres, and around 1% for parks and gardens. It should be noted that these figures probably underestimate the prevalence of *P. ramorum*, as checks are not carried out unannounced and samples for analysis are only taken from symptomatic plants. The detection of outbreaks has declined sharply since 2008 (Figure 25). By comparison, in England and Wales, 321 outbreaks of *P. ramorum* had been detected between 2002 and 2004 during 1761 inspections in nurseries and garden centres, and 60 outbreaks during 1367 inspections in parks, gardens and natural sites (DEFRA, 2005).

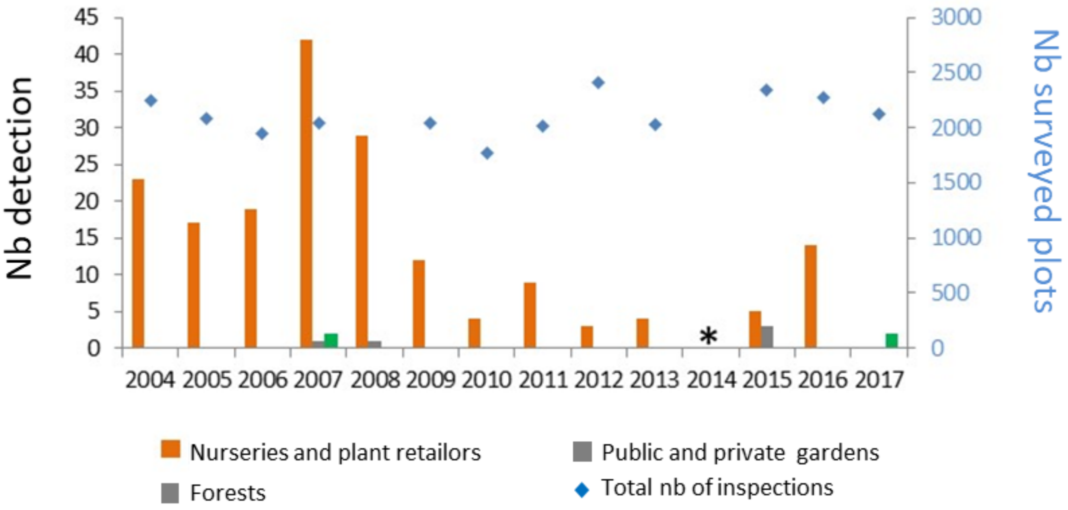


Figure 25: Detections of *Phytophthora ramorum* following official inspections (data on cases reported at EU level, provided by the DGAL (French Ministry of Agroculture); * = no data)

Many of the nurseries detected as contaminated in France between 2004 and 2017 are located in the Brittany coastal area and in the Pays de la Loire region (Figure 26). *P. ramorum* was thus detected in 216 production or resale sites, mainly on rhododendron and *Viburnum tinus*. The origin of the infected material is rarely stated (less than one third of identified origins). It is therefore impossible to study the origin of the infected material more precisely; in some cases the material had been purchased in Belgium. Eradication at production or resale sites, where positive detection of *P. ramorum* has been obtained in France, is rarely effective: in more than 25% of these sites, a new case was detected within a few years after the first one. Recurrent detection of *P. ramorum* has also been reported in several nurseries in Switzerland, and may be explained either by new introductions or eradication failures (Prospero *et al.*, 2013).

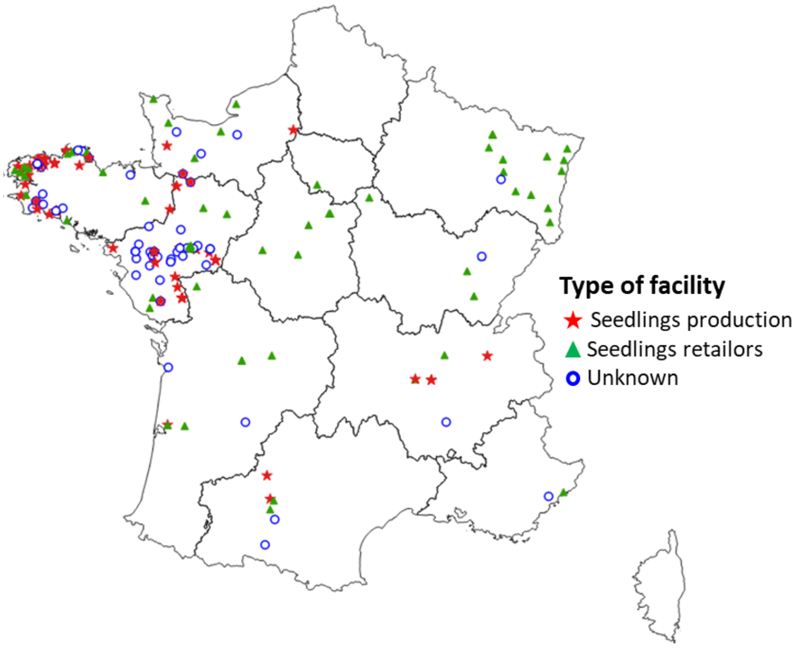


Figure 26: Location of nurseries where *Phytophthora ramorum* was detected between 2004 and 2017 (data provided by the DGAL- French Ministry of Agriculture)

The decisive role of introductions of contaminated plants in the subsequent development of epidemics in the wild is well documented for California, with several studies based on genetic analyses of *P. ramorum* populations to reconstruct the history of the invasion (Mascheretti *et al*., 2008 and 2009). The most comprehensive study (Croucher *et al*., 2013) used an intensive sampling of 832 *P. ramorum* isolates from 13 nurseries and 60 forest sites, genotyped with nine microsatellite loci, and a coalescence network approach with Bayesian inference. It appears that "nursery genotypes" generated the entire network and that the observed distribution of *P. ramorum* in California is explained by multiple independent introductions (and not by a gradual spread from one or two introduction points), suggesting a significant number of introductions related to the movement of infected plants, both at short and long distances.

The spatio-temporal distribution of reports of *P. ramorum* in Great Britain also suggests that the inoculum causing the forest epidemic may have come from initial epidemics in nurseries (detected since the early 2000s), relayed by *Rhododendron ponticum* infections in parks and natural environments (Tracy, 2009), preceding the first reports on larch (2009). The same type of spatio-temporal pattern seems to apply for Ireland, according to the analysis of detection data following official inspections, with first reports on rhododendron in nurseries and almost simultaneously in the environment, preceding by a few years the detections in larch plantations (Figure 27, with data from O'Hanlon, 2016).

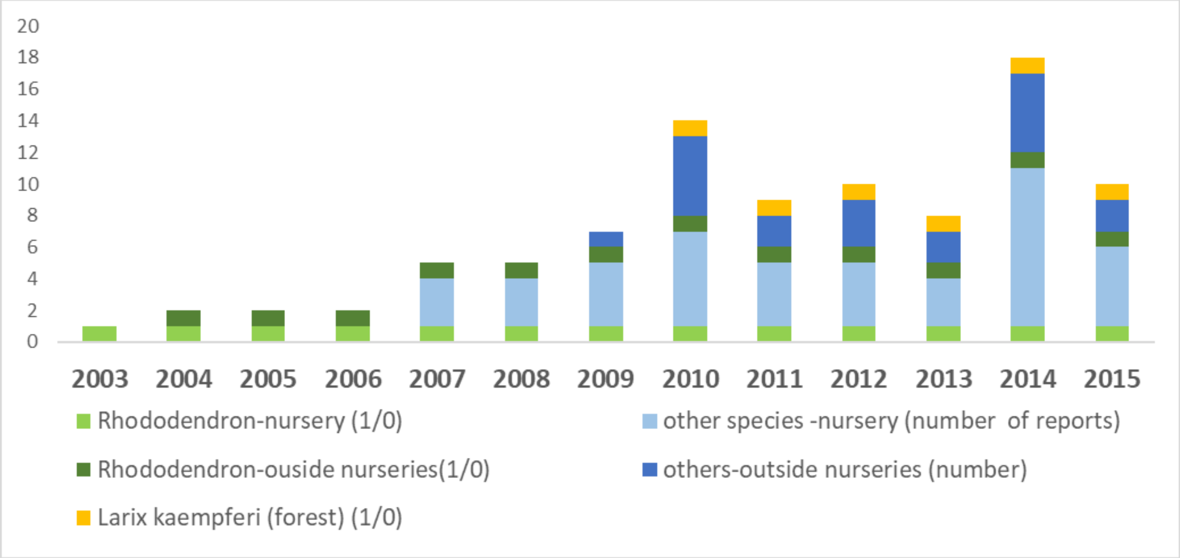


Figure 27: Summary of *Phytophthora ramorum* detections in the Republic of Ireland between 2003 and 2015 on different species and in different types of environment (data from O'Hanlon *et al*., 2016)- For Rhododendron and Larix, coloured rectangles represent positive detection, for other species, in or outside nurseries, the size of the rectangle corresponds to the number of positive cases

Although the transmission from nursery to the wild rhododendron compartment and then to the forest compartment cannot be formally demonstrated, a strong positive correlation has been observed for England and Wales between the location of nursery and semi-natural outbreaks within a radius of 1 km for the period 2003-2006 (Xu *et al*., 2009). Chadfield and Pautasso (2012), using DEFRA data over a longer period (2002-2009), showed a positive correlation between the incidence of *P. ramorum* in gardens or natural environments and the detection of *P. ramorum* in commercial channels. It therefore appears that nurseries and garden centres are high-risk sites for the introduction and spread of *P. ramorum* in the wild.

Once present in the natural environment, *P. ramorum* can be dispersed via soil, especially by various human activities (Davidson *et al*., 2005). A statistical link between the density of human activities (walking, hiking, etc.) and the frequency of detection of *P. ramorum* has been demonstrated at different spatial scales in California (Cushman and Meentemeyer, 2008; Davidson *et al*., 2005).

6 Conclusions of the Working Group

6.1 Classification of species susceptibility

We propose a new terminology for classifying species susceptibility, to avoid confusion between types of symptoms and epidemiological role, and ambiguities from terms used differently by different communities of pathologists. The terminology used here differentiates two components of susceptibility: **vulnerability** (related to the expression and severity of symptoms on different organs) and **competence** (related to the epidemiological role of transmission of the pathogen, via its sporulation), which may interact (Figure 8).

Based on the available data, we assessed these two components for the 136 forest tree species in France (including the 66 regulated species) using five categories from "not significant" to "high" (Tables 2, 3, 4, 5; Figures 9, 10, 11). Competence was also assessed for the 47 most common forest shrub species found in French forests (Tables 6, 8). **However, it should be stressed that these assessments were often associated with moderate to high uncertainties**. Lastly, a list of natural ornamental host species of *P. ramorum* was produced (Table 7).

- At the top of the vulnerability and competence ranking were **the three *Larix* species** *(L. kaempferi, L. decidua, L. x eurolepis*), which could not be distinguished from each other after a thorough analysis of all the available data. However, while uncertainty was low concerning *L. kaempferi*, for which the epidemic is proven, it was moderate for the other two species, for which the field data are very partial.
- The case of **sweet chestnut** is of great concern. We assessed its vulnerability and competence as moderate to high, but there are still moderate uncertainties. The situation concerning this species has recently changed in Great Britain. If it were confirmed that *P. ramorum* sporulation on sweet chestnut is sufficient to cause multiple auto-infections ultimately leading to decline (with vulnerability increasing to high) and to actively contribute to the pathogen's multiplication and transmission (causing competence to increase to high), the economic and environmental risk posed by *P. ramorum* would be considerably greater given the importance of *Castanea sativa* in France.
- Among the other forest species, some **oaks** (*Q. ilex, Q. cerris* and *Q. rubra*) have moderate to high vulnerability and moderate or moderate to high competence (for *Q. ilex*), and should therefore be considered with caution. Fortunately, according to current knowledge, sessile and pedunculate oaks have only low to moderate vulnerability and not significant competence. **Beech** has higher vulnerability (in the form of trunk cankers) but this can only be expressed in the presence of a high inoculum produced on other species acting as competent hosts. Among the conifers, **Douglas fir, Sitka spruce and grand fir** can express relatively severe symptoms (current season's shoot dieback), but numerous observations in North America and Great Britain have shown that their competence is not significant (examples of non sporulating "foliar hosts”). As with beech, therefore, damage is only observed in situations of high inoculum produced by other species having significant competence.
- Lastly, it is necessary to mention a number of species with competence estimated as moderate to high: **ash, black locust (false acacia) and strawberry tree**.

6.2 Risk mapping

The risk mapping model by Meentemeyer *et al.* (2004), already used in Sansford *et al.* (2009), was chosen because it can integrate the effects of both climate and the competence of vegetation. **Several improvements were made with respect to RAPRA** (Sansford *et al.*, 2009) to adapt this model to France, concerning: i) the level of spatial resolution of the meteorological data used, ii) the extension of the score calculation period to cover the whole year in order to take the sporulation period into account (which is different in Europe and the United States), iii) the consideration of relative humidity, and iv) the competence of plant communities in forests (not taken into account in RAPRA due to a lack of data over Europe). It should be pointed out that major **sources of uncertainty** remain regarding the determinants of the risk posed by *P. ramorum*, whether in terms of the ability of woody vegetation to multiply inoculum and enable persistence of the oomycete (competence), or of certain climate components (impact of severe winters on winter survival and on the level of primary inoculum at the beginning of the season). It can also be added that there is genetic and phenotypic diversity in *P. ramorum* (Dodd *et al*., 2015) and variation in susceptibility within host species (Hayden *et al*., 2011; Cobb *et al*., 2018), which will inevitably increase uncertainty in the model predictions.

Despite this, some fairly clear conclusions emerge from this study.

Competence of vegetation

We did not identify any understory woody plants with high competence and high regional frequency that might play the same epidemic role as California bay laurel in the western United States or rhododendron (*R. ponticum*) in Great Britain (Purse *et al*., 2013). Rhododendron are generally rare in French forests. There are areas in the eastern Languedoc (Gard) and in Corsica where the frequency of holm oak, sweet chestnut, strawberry tree, *Viburnum tinus* and *Rhamnus alaternus* gives the vegetation high competence, but the climate in these areas is not favourable to *P. ramorum* (see below). The Alpine larch forest is another area with high vegetation competence. However, our study confirmed RAPRA's conclusions on this point: the climate of this area is not favourable to *P. ramorum*. **For the rest of France, the average vegetation competence is moderate (Figure 12)**. **However, this result must be placed in perspective**:

(i) Sweet chestnut was identified as a forest species at risk of *P. ramorum* outbreaks (Denman *et al*., 2005b, Webber *et al*., 2017). Indeed, sweet chestnut stands far away from other inoculum sources such as larch or rhododendron have been affected in southern Britain and are declining from year to year, suggesting that this species may have significant competence. In Great Britain, sweet chestnut is relatively uncommon (fewer than 20,000 ha in 2000; Braden and Russell, 2001), especially in areas favourable to *P. ramorum*. However, in France, sweet chestnut is the fourth most common deciduous species for standing timber volume (5% of the French forest total) with more than 700,000 hectares (IFN 2014 *La Forêt en Chiffres et en Cartes* [The forest in figures and maps]). Sweet chestnut is common in areas with a climate favourable to *P. ramorum* such as Brittany, Limousin, Montagne Noire, the Pyrenean foothills, Cévennes and eastern Isère. Underestimating the competence of sweet chestnut would have serious consequences on our conclusions (Figure 21). This is probably the major risk in our country, but still with a high level of uncertainty.

(ii) Competence maps represent an average situation, with values interpolated using IFN sampling data. They do not therefore provide information on any possible local risk associated with the existence of stands with high competence and high vulnerability such as Japanese larch.

(iii) The vegetation competence maps that were produced only concern forest stands. Our knowledge of the frequency of plant species outside forests is too limited to allow further analysis. In particular, we have found that there is inadequate knowledge of hedges and highly anthropised environments such as parks and gardens, which could play a significant role when they are close to forests. For sweet chestnut, orchard data should also be taken into account.

Areas with a favourable climate

Our study enabled predictions to be refined on areas of France with a favourable climate for the development of *P. ramorum*, compared to previous studies. The use of meteorological data with a finer spatial resolution than that used in RAPRA enabled better consideration of hydric parameters (precipitation, relative humidity), which have a decisive role in the epidemiology of *P. ramorum*. On the other hand, Meentemeyer's model had to be adapted to take into account the sporulation period of *P. ramorum*, which is different in Europe compared to North America.

These changes led to large differences for areas favourable to *P. ramorum* in France compared to what was indicated in RAPRA with the same model. **In addition to western France (Brittany, Limousin, Pyrenean foothills) and the coastal area along the Channel, many medium altitude**

areas appear to be climatically favourable to *P. ramorum*, in the south (Montagne Noire, Cévennes) and in the east (Vosges and Jura) (Figure 20). While the mountainous massifs of Eastern France do not include vegetation with high competence, this is not the case in the Montagne Noire and Cévennes, where the significant presence of sweet chestnut makes the situation problematic (Figure 23). The areas where larch is planted in France, according to the DSF's (French Forest Health Department) "plantation" survey, generally have a climate favourable to *P. ramorum* (Figure 23). The Mediterranean area seems to be unfavourable to the development of *P. ramorum*, contrary to what could be suggested from rough "climate matching" projections with California (Sansford *et al*., 2009).

6.3 Synopsis: what scenario leads to an epidemic situation?

The analysis of recent epidemics caused by *P. ramorum* in the United States and Europe (United Kingdom and Ireland) shows a certain level of unpredictability, due to accidental introductions and the ability of this pathogen to adapt to numerous hosts and environments. However, some common characteristics make it possible to develop a **"most plausible scenario" leading to these outbreak situations, with three main stages**:

(1) Accidental introduction and transport of *P. ramorum* via plant trade, particularly rhododendron and other ornamental species;
(2) Multiplication in semi-natural or natural environments, particularly forests, on highly competent hosts such as California bay laurel or *Rhododendron ponticum*;
(3) Outbreaks on forest trees, whose expansion is determined by the presence of susceptible hosts (high vulnerability and competence) and favourable climatic conditions.

This scenario is supported by a number of genetic and epidemiological studies (Xu *et al*., 2009; Chadfield and Pautasso, 2012; Croucher *et al*., 2013; O'Hanlon, 2016).

It can be hypothesised that the successive and increasingly frequent appearance (detection) of *P. ramorum,* first on ornamental plants in nurseries, then on shrubs (related to ornamental species or varieties) in forests and finally on forest trees, corresponds to a gradual increase and diversification of its population, becoming increasingly free from the anthropised environments favourable to its establishment and multiplication. This dynamic, accompanied by a lag phase of varying length between its presence in a controlled environment (e.g. gardens) and its escape into the wild, is typical of many invasive alien species, including plants (Sakai *et al.*, 2001). An important point in this dynamic is that the spatial expansion observed in the natural environment can be very rapid after the initial reports in that environment, strongly affecting the chances of successful eradication (Hansen *et al*., 2008; Harwood *et al.*, 2009; Parnell *et al*., 2010; Cunniffe *et al*., 2016). Several reasons explain the speed of the epidemic: multiple introductions, population dynamics (exponential start), under-sampling (no systematic surveillance before the first reports, which are only the tip of the iceberg, with other small outbreaks possibly going unnoticed) (Filipe *et al.*, 2012), an increase in long-distance dispersal events with the population size (Croucher *et al*., 2013), adaptive phenomena in the invasive species over time (Sakai *et al*., 2001; Croucher *et al*., 2013; Robin *et al*., 2017), and the very high susceptibility of naïve hosts, i.e. those never before confronted with the pathogen (Garbelotto and Hayden, 2012). This rapid expansion can be illustrated by the case of Scotland, where the first outbreak of *P. ramorum* was observed on larch in November 2010, during surveillance missions following its discovery in England. After two autumns and winters regarded as favourable (rainy and mild) in an area of extensive larch stands, 5000 to 6000 ha were infected in 2013 (Forestry Commission Scotland website).

It can be seen that the outbreaks in larch plantations in the Sizun area of Brittany (Finistère) seem to correspond closely to this general scenario (Figure 28). Indeed, they are located in a high-risk area, which combines both a high density of rhododendron production nurseries with early reports of *P. ramorum* detection (each year since 2002), the highest density of rhododendron in French forests (even if its abundance remains relatively low), detections of *P. ramorum* on rhododendron in forest areas (since 2007, in Finistère and Morbihan, DSF database, although this presence has not been confirmed by subsequent sampling in the same area), a favourable climate and the presence of Japanese larch.

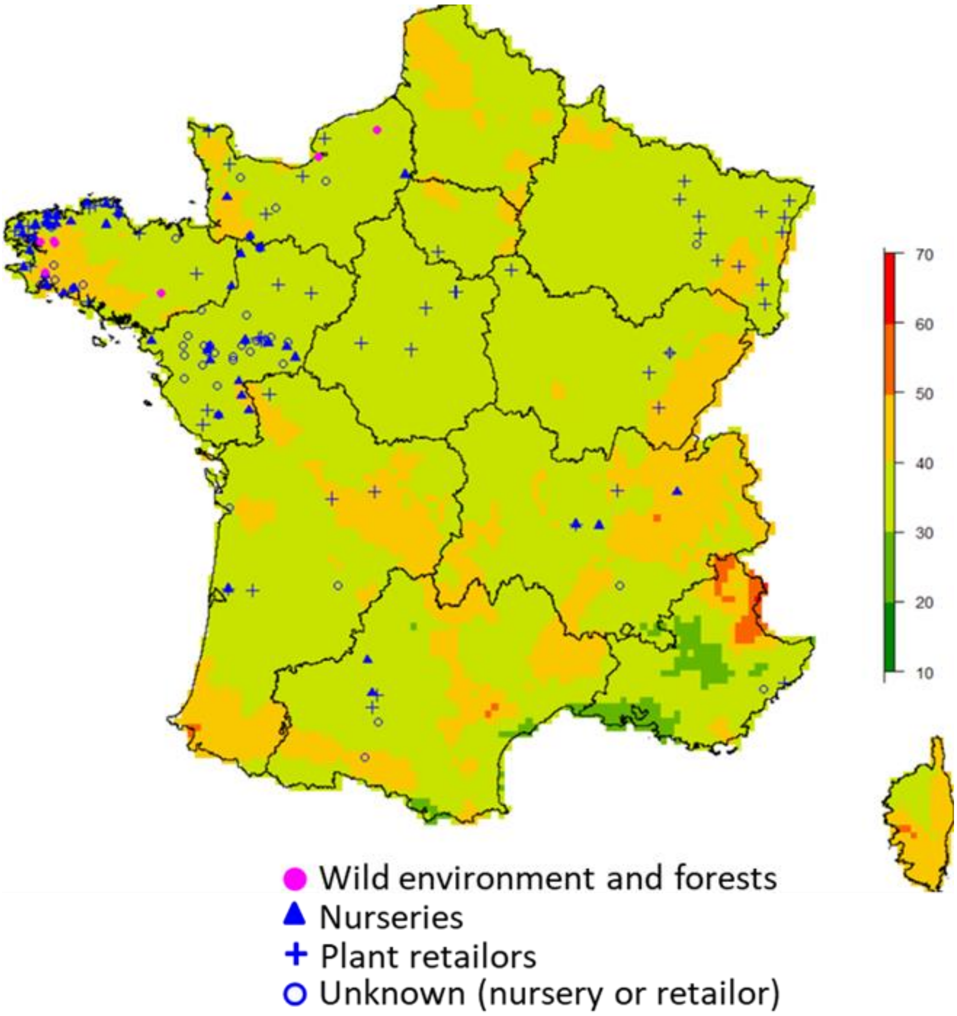


Figure 28: Location of the identified points where *P. ramorum* is present in France on the *P. ramorum* risk map, integrating climatic variables and competence (map created with the 95% quantile of the competence map)

6.4 Recommendations

6.4.1 Practical recommendations

Eradication

According to the scenario described above, management of the "Brittany outbreak" is of paramount importance. Based on the British experience, DSF has carried out a careful surveillance targetting *P. ramorum* over the past few years. This gives reason to hope that one of the first outbreaks in the forest environment has been detected, in a phase where disease progression is still slow. Moreover, given the relatively low abundance of rhododendron in the forest, epidemic relays are limited. Unlike the British case, therefore, eradication has to be considered, by eliminating not only larch but also "wild" rhododendron in the affected area. The invasive alien species status of *R. ponticum* in Brittany and its epidemic role for *P. ramorum* justify taking measures to eliminate this species in forests before it reaches population levels comparable to those in the United Kingdom. Eradication procedures should also be accompanied by hygiene measures to limit the spread of *P. ramorum* via tools, vehicles, technical staff and inspectors. The spread of *P. ramorum* by logs from infected trees is unlikely. Indeed, Davidson *et al.* (2005, 2008) showed that *P. ramorum* sporulation was not observed from intact bark of *Quercus* sp. or *Notholithocarpus densiflorus*. Sporulation from *N. densiflorus* was only observed on the bark of small diameter stems (<5 cm, chlamydospores and sporangia) or large-diameter wounded stems (chlamydospores only, when the phloem was exposed). On this basis, the British do not take any special precautions when transporting infected larch logs, but treat them separately in "approved" sawmills where the logs are debarked and the bark composted (Forestry Commission website).

In addition to eradication measures, it would be advisable to develop information campaigns aimed at the public, forest owners and professionals, as has been done in the Netherlands for example (de Gruyter and Steegs, 2006). Alexander and Lee (2010) also stressed the importance of information campaigns/mobilisation of all the parties in California.

Forest surveillance

Aside from the outbreak, very detailed surveillance of the **Brittany** area on larch, rhododendron and sweet chestnut is highly recommended. In order of priority, the intensity of surveillance should then focus on the **Normandy and Limousin** regions. The first combines larch plantations, relatively favourable climate and competence (Figure 25), and detection of *P. ramorum* in nurseries and for the first time in the wild on rhododendron in 2007 (Calvados) and then again in 2014 (Seine Maritime) (N. Schenck, LNPV-MAF Report, 2007; detections not confirmed by subsequent sampling in the same areas). Limousin is strongly concerned due to its larch plantations, particularly *L. kaempferi*, and also has rather favourable climate and competence. More generally, special attention should be paid to all larch plantations (regardless of species) in areas with a climate favourable to *P. ramorum* and **any suspicion regarding sweet chestnut** should be investigated by screening for *P. ramorum*. The use of rapid field immunological tests (Pocket Diagnostic® LFD test, a registered trademark of Abingdon Health, UK), specific to the genus *Phytophthora* and applicable to leaves or branches is particularly interesting in this regard because it enables more effective targeting of samples to be sent to the laboratory for validation and species identification.

Nursery surveillance

The role of the plant trade from and between nurseries in the spread of plant pathogens, especially *Phytophthora* and particularly *P. ramorum*, is now very well established (Jung *et al*., 2016; Liebhold *et al*., 2012; Migliorini *et al*., 2015). This applies not only to forest plants but also, and sometimes even more so, to ornamental plants, as clearly illustrated by the case of *P. ramorum*. This raises the question of regulatory changes aimed at prohibiting imports of certain species whose risk/benefit ratio is too high (https://www.iufro.org/science/divisions/division-7/70000/publications/montesclaros-declaration/). For instance, *Notholithocarpus densiflorus* and *Umbellularia californica* are in the French nursery catalogue.

Checks of nurseries, garden centres, parks and gardens, especially in areas with a favourable climate and environment for *P. ramorum*, are of paramount importance and must be improved. Upstream, good practices to limit the risks of contamination of plant material and potting media by *P. ramorum* should be promoted in nurseries, avoiding the use of fungicidal treatments that only mask symptoms. Different types of approaches are possible, either following a traditional approach (a reactive method based on inspections of control points and material produced) or a systems approach (a proactive method based on the implementation of procedures and audits, and prevention, Parke and Grünwald, 2012).

Many studies have highlighted the diversity of *Phytophthora* spp. communities in nurseries, and the main control points from which samples should be taken are now known: in fact, the entire production chain and all inputs are involved (Parke and Grünwald, 2012). It seems essential to test not only plants with leaf necrosis but also asymptomatic plants, since *P. ramorum* can cause latent infections (Migliorini *et al*., 2015). The list of species to be monitored should be updated regularly based on knowledge of susceptible species. Following any positive detections, it is imperative to implement strict eradication measures on outbreaks in these sites and to verify their effectiveness.

Surveillance of nurseries, garden centres and non-forest environments should be carried out according to an effective sampling and data collection plan. Quality surveillance data (on presence and absence) that are georeferenced, validated and incorporated into databases built according to standard practices are necessary for any epidemiological work. A database meeting these criteria is already available for observations concerning forests that are the responsibility of the DSF. However, data on nursery surveillance have been more difficult to obtain and do not meet the criteria outlined above, despite this being a crucial area for surveillance and therefore management of forest pathogens. Lastly, this still leaves all the private spaces (parks, gardens) or spaces outside forests (non-forested areas, avenue trees, hedges, orchards, etc.) that can act as relays for the infection of forest trees, and for which data are extremely partial or non-existent.

Reforestation in risk areas

Larch plantations, particularly those with hybrid larches, are currently becoming more and more widespread (Figure 2). Although it has not been fully demonstrated that the susceptibility of European and hybrid larch (especially for the marketed varieties) is as high as that of Japanese larch, caution should be exercised and the risk associated with *P. ramorum* should be taken into account more than ever, especially in areas identified as having a favourable climate. According to the current state of knowledge, the creation in these areas of large stands of hosts with proven susceptibility seems risky.

In general, our classification for species susceptibility is consistent with the Forestry Commission's recommendations for planting in risk areas. Thus, among the 13 regulated species in France that we assessed with moderate to high vulnerability and/or competence, 10 are considered "at risk" or even to be avoided (for the three species of larch), while the other three are not or are only rarely planted in Great Britain.

6.4.2 Knowledge gaps – Research questions

The level of susceptibility of **European and hybrid larch**, particularly of the marketed varieties (forest reproductive material = FRM), of parents used in seed orchards, or of other material included in the plant breeding programme, has not been characterised. It would be highly desirable to assess this material's susceptibility, under containment conditions and/or in collaboration with Great Britain under natural *P. ramorum* inoculum conditions.

Concerning species susceptibility, the greatest unknown concerns **sweet chestnut**, whose levels of competence (ability to promote *P. ramorum* sporulation) and vulnerability (development of multiple infections, extension from leaves to branches, etc., potentially leading to tree decline) remain to be determined, following the recent observations in Great Britain (Webber *et al*., 2017).

Lastly, several questions remain concerning **the epidemiology of *P. ramorum* in the wild**. Additional studies are required to gain a better understanding of the oomycete's latency and survival capacity in the environment (particularly in litter), especially from one season to the next, as well as the effect of winter temperatures, potential woody reservoirs and the spatio-temporal dynamics of the inoculum, including vertical propagation to tree crowns, "long-distance" dispersal, etc. *P. ramorum* should be screened for in all ecosystem compartments in the affected area in Brittany. The genetic study of available isolates, and any others that may be obtained in the future, facilitated by the availability of a complete version of the genome sequence (Tyler *et al*., 2006) could enable the history of the invasion to be reconstructed, in particular to test the scenario of transition from nurseries to wild hosts and then to larch.

Date of validation of the collective expert appraisal report by the Working Group and the Expert Committee: 13/11/2018

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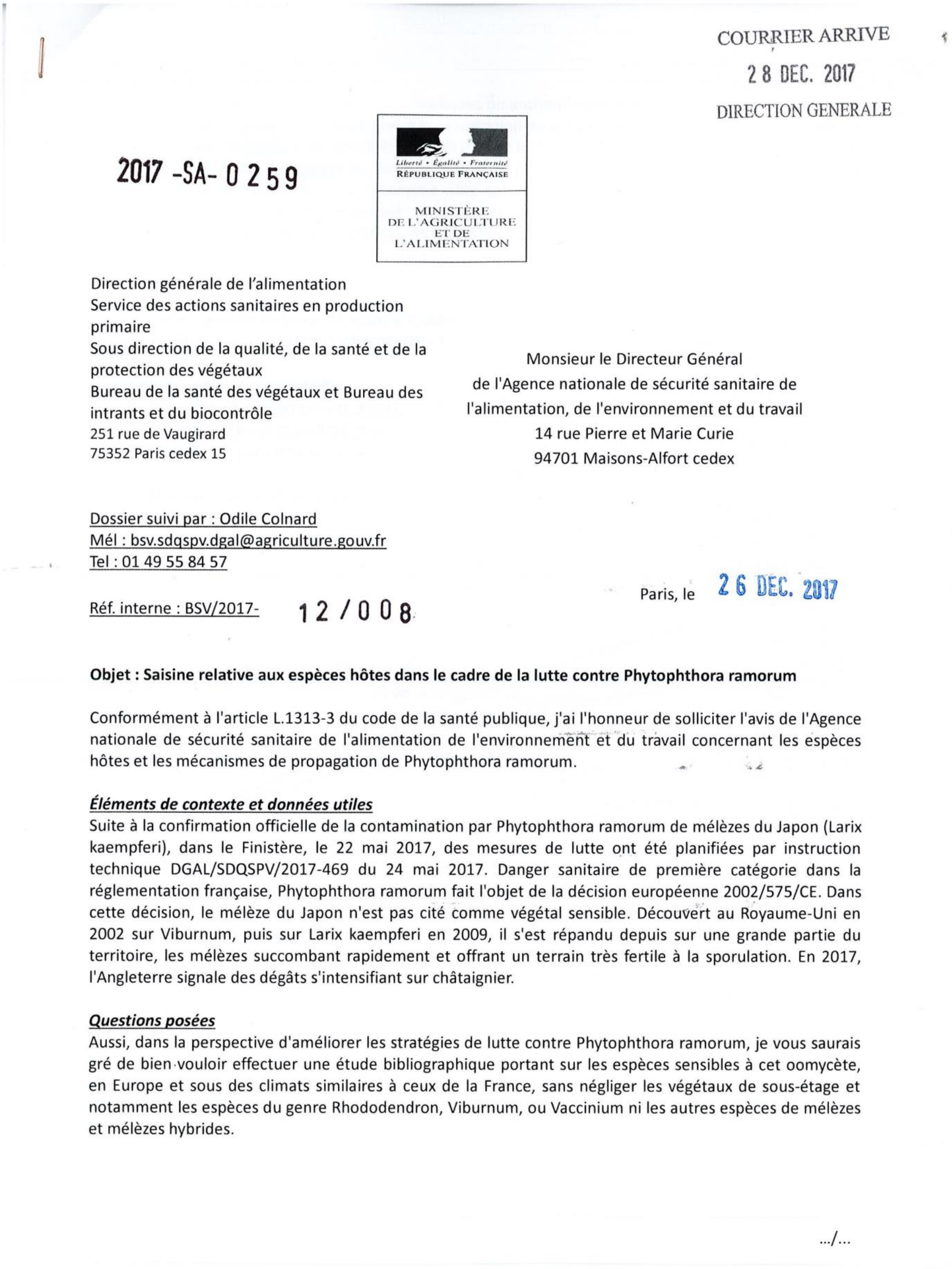
7.2 Legislation and Regulations

Ministerial Order of 15 December 2014 on the list of Category 1 and 2 health hazards for plant species. Official Journal of the French Republic no. 0298 of 26 December 2014, page 22318, text no. 121.

ANNEXES

Annex 1: Formal request letter



COURRIER ARRIVE
28 DEC. 2017
DIRECTION GENERALE

2017 -SA- 0259

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MINISTÈRE
DE L'AGRICULTURE
ET DE
L'ALIMENTATION

Direction générale de l'alimentation
Service des actions sanitaires en production primaire
Sous direction de la qualité, de la santé et de la protection des végétaux
Bureau de la santé des végétaux et Bureau des intrants et du biocontrôle
251 rue de Vaugirard
75352 Paris cedex 15

Monsieur le Directeur Général
de l'Agence nationale de sécurité sanitaire de
l'alimentation, de l'environnement et du travail
14 rue Pierre et Marie Curie
94701 Maisons-Alfort cedex

Dossier suivi par : Odile Colnard
Mél : bsv.sdqspv.dgal@agriculture.gouv.fr
Tel : 01 49 55 84 57

Paris, le 26 DEC. 2017

Réf. interne : BSV/2017- 12/008

Objet : Saisine relative aux espèces hôtes dans le cadre de la lutte contre Phytophthora ramorum

Conformément à l'article L.1313-3 du code de la santé publique, j'ai l'honneur de solliciter l'avis de l'Agence nationale de sécurité sanitaire de l'alimentation de l'environnement et du travail concernant les espèces hôtes et les mécanismes de propagation de Phytophthora ramorum.

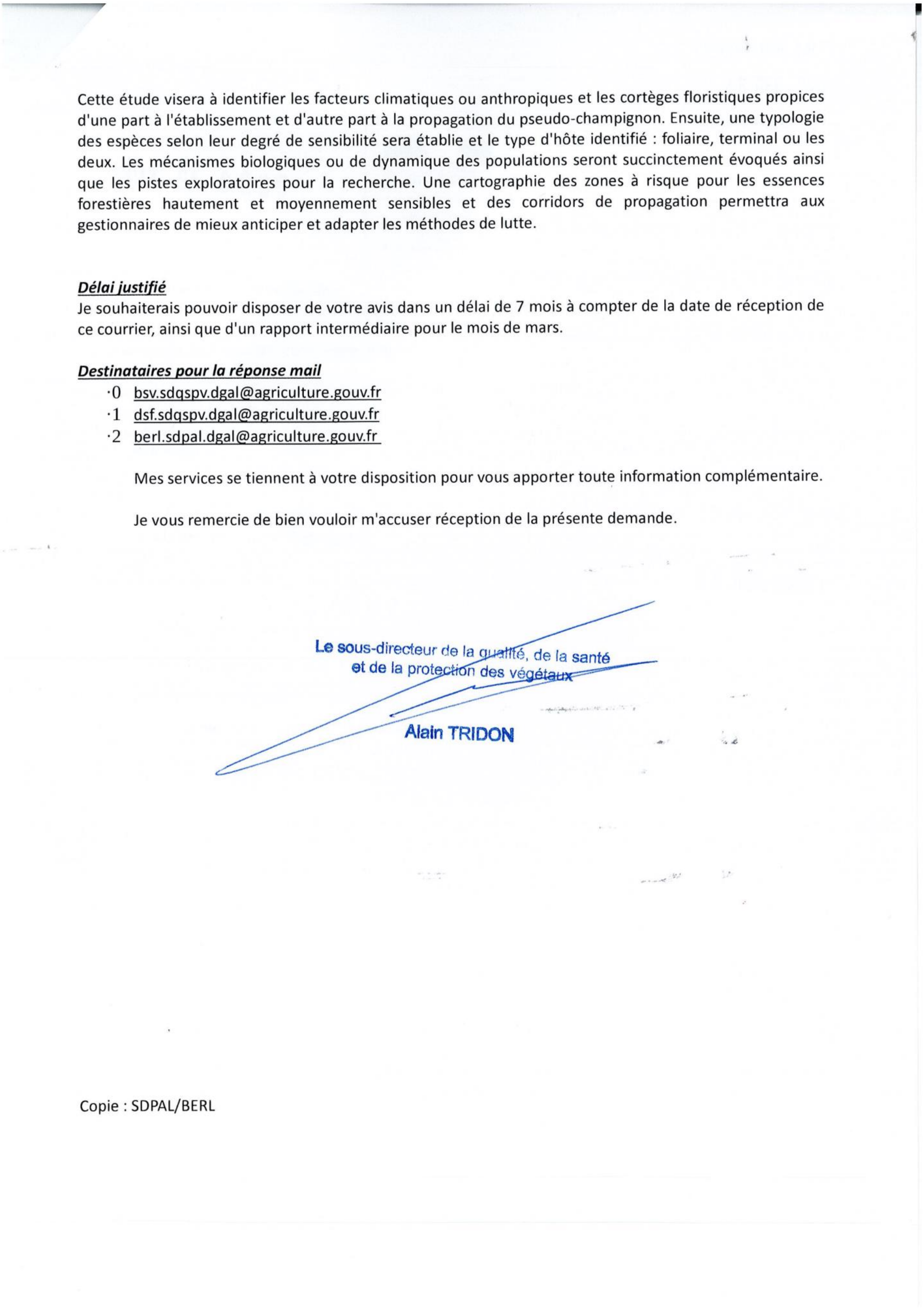
Éléments de contexte et données utiles

Suite à la confirmation officielle de la contamination par Phytophthora ramorum de mélèzes du Japon (Larix kaempferi), dans le Finistère, le 22 mai 2017, des mesures de lutte ont été planifiées par instruction technique DGAL/SDQSPV/2017-469 du 24 mai 2017. Danger sanitaire de première catégorie dans la réglementation française, Phytophthora ramorum fait l'objet de la décision européenne 2002/575/CE. Dans cette décision, le mélèze du Japon n'est pas cité comme végétal sensible. Découvert au Royaume-Uni en 2002 sur Viburnum, puis sur Larix kaempferi en 2009, il s'est répandu depuis sur une grande partie du territoire, les mélèzes succombant rapidement et offrant un terrain très fertile à la sporulation. En 2017, l'Angleterre signale des dégâts s'intensifiant sur châtaignier.

Questions posées

Aussi, dans la perspective d'améliorer les stratégies de lutte contre Phytophthora ramorum, je vous saurais gré de bien vouloir effectuer une étude bibliographique portant sur les espèces sensibles à cet oomycète, en Europe et sous des climats similaires à ceux de la France, sans négliger les végétaux de sous-étage et notamment les espèces du genre Rhododendron, Viburnum, ou Vaccinium ni les autres espèces de mélèzes et mélèzes hybrides.

.../...



Cette étude visera à identifier les facteurs climatiques ou anthropiques et les cortèges floristiques propices d'une part à l'établissement et d'autre part à la propagation du pseudo-champignon. Ensuite, une typologie des espèces selon leur degré de sensibilité sera établie et le type d'hôte identifié : foliaire, terminal ou les deux. Les mécanismes biologiques ou de dynamique des populations seront succinctement évoqués ainsi que les pistes exploratoires pour la recherche. Une cartographie des zones à risque pour les essences forestières hautement et moyennement sensibles et des corridors de propagation permettra aux gestionnaires de mieux anticiper et adapter les méthodes de lutte.

Délai justifié

Je souhaiterais pouvoir disposer de votre avis dans un délai de 7 mois à compter de la date de réception de ce courrier, ainsi que d'un rapport intermédiaire pour le mois de mars.

Destinataires pour la réponse mail

·0 bsv.sdqspv.dgal@agriculture.gouv.fr
·1 dsf.sdqspv.dgal@agriculture.gouv.fr
·2 berl.sdpal.dgal@agriculture.gouv.fr

Mes services se tiennent à votre disposition pour vous apporter toute information complémentaire.

Je vous remercie de bien vouloir m'accuser réception de la présente demande.

Le sous-directeur de la qualité, de la santé
et de la protection des végétaux

Alain TRIDON

Copie : SDPAL/BERL

Agence nationale de sécurité sanitaire
de l'alimentation, de l'environnement et du travail
14 rue Pierre et Marie Curie
F94701 Maisons-Alfort cedex
www.anses.fr
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