An Overview of Canadian Research Activities on Diseases Caused by *Phytophthora ramorum*: Results, Progress, and Challenges

Simon Francis Shamoun†
Natural Resources Canada (NRCan), Canadian Forest Service (CFS), Pacific Forestry Centre (PFC), Victoria, BC, V8Z 1M5, Canada
Danny Rioux
NRCan, CFS, Laurentian Forestry Centre (LFC), P.O. Box 10380, Sainte-Foy, Québec, G1V 4C7, Canada
Brenda Callan
NRCan, CFS, PFC, Victoria, BC, V8Z 1M5, Canada
Delano James
Canadian Food Inspection Agency (CFIA), Sidney Laboratory, Sidney, BC, V8L 1H3, Canada
Richard C. Hamelin
NRCan, CFS, LFC, P.O. Box 10380, Sainte-Foy, Québec, G1V 4C7, Canada
Guillaume J. Bilodeau
CFIA, P.O. Box 11300, Ottawa, ON, K2H 8P9, Canada
Marianne Elliott
NRCan, CFS, PFC, Victoria, BC, V8Z 1M5, Canada
C. André Lévesque
Agriculture and Agri-Food Canada (AAFC), Ottawa, ON, K1A 0C6, Canada
Elisa Becker
NRCan, CFS, PFC, Victoria, BC, V8Z 1M5, Canada
Dan McKenney and John Pedlar
NRCan, CFS, Great Lakes Forestry Centre (GLFC), Sault Ste. Marie, ON, P6A 2E5, Canada
Karen Bailey
AAFC, Saskatoon, SK, S7N 0X2, Canada
S. C. Brière
CFIA, P.O. Box 11300, Ottawa, ON, K2H 8P9, Canada
Kurt Niquidet and Eric Allen
NRCan, CFS, PFC, Victoria, BC, V8Z 1M5, Canada

International trade and travel are the driving forces behind the spread of invasive plant pathogens around the world, and human-mediated movement of plants and plant products is now generally accepted as the primary mode of their introduction, resulting in huge disturbance to ecosystems and severe socio-economic impact (Liebhold et al. 2012; Santini et al. 2013). These problems are exacerbated under the present conditions of rapid climatic change (Brasier 2008; Hansen 2008; Sturrock et al. 2011).

We report an overview of the Canadian research activities on *Phytophthora ramorum* Werres, de Cock & Man in't Veld (Werres et al. 2001). Since the first discovery and subsequent eradication of *P. ramorum* on infected ornamentals in nurseries in Vancouver, British Columbia, in 2003, a research team of Canadian government scientists representing Canadian Forest Service (CFS), Canadian Food Inspection Agency (CFIA), and Agriculture and Agri-Food Canada (AAFC) worked together over a 10-year period and have significantly contributed to many aspects of research and risk assessment on this pathogen. The overall objectives of the Canadian research efforts were to gain a better understanding of the molecular diagnostics of *P. ramorum*, its biology, host-pathogen interactions, and management options. With this information it was possible to develop pest risk assessments (PRA) and evaluate the environmental and economic impact and future research needs and challenges relevant to *P. ramorum* and other emerging forest *Phytophthora* spp.

Current address of R. C. Hamelin: University of British Columbia, Department of Forest and Conservation Sciences, Vancouver, BC V6T 1Z4, Canada. Current address of M. Elliott: Washington State University, Puyallup Research and Extension Centre, Puyallup, WA 98371-4998, USA. Current address of K. Niquidet: Bank of Canada, Ottawa, ON K1A 0G9, Canada.

†Corresponding author: Simon Francis Shamoun;
E-mail: Simon.Shamoun@Canada.ca

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Phytophthora Forest Diseases

Phytophthora spp. cause diseases that result in devastating losses to a wide variety of plants. Diseases such as root and crown rots, cankers, foliar blights, and fruit rots, affect food and fiber crops, forest trees, and a variety of ornamental plants around the world (Agrios 2005; Brasier 2008; Erwin and Ribeiro 1996). The genus *Phytophthora* currently affects more than 130 known host plant species, and is probably the world's most destructive group of plant pathogens. Precipitated by the discovery of *P. ramorum*, more than 50 new species were identified worldwide during the last decade.

The known host range of *P. ramorum* has greatly expanded since its initial discovery in Europe and the United States and phytosanitary regulatory agency websites in Canada, the E.U., and the U.S. display the updated host lists. The known host range includes many woody evergreen hosts that are native or established in forested and urban areas in the west coast of the U.S. and Canada. *P. ramorum* is usually nonlethal on these foliar hosts, which can serve as potential

reservoirs for *P. ramorum* inoculum. Infection of these hosts increases the risk of spread to more susceptible hosts, especially through nursery trade operations (APHIS-PPQ 2013; CFIA 2015; Grünwald et al. 2008; Kristjansson and Miller 2009).

Current Status of *P. ramorum* in Canada

In Canada, the CFIA first confirmed the presence of *P. ramorum* in rhododendron plants in a south-coastal British Columbia (BC) nursery during their national survey in 2003 (Fig. 1). Since then, the pathogen has occasionally been detected in a few nurseries in the south BC mainland and on Vancouver Island. When *P. ramorum* was detected, measures were immediately taken to decontaminate the site under CFIA's supervision. To date, there has been no wildland detection of *P. ramorum* in Canada (Kristjansson and Miller 2009), a situation similar to that occurring in the eastern U.S. where *P. ramorum* has been eradicated in ornamental nurseries without allowing its establishment in nature.

Canadian Pest Risk Analyses and Economic Impact

Impact of *P. ramorum* and risk assessment in Canada. Policies in Canada and the U.S. for regulating and mitigating *P. ramorum* are quite similar. *P. ramorum* has been under regulation in Canada and the U.S. since 2003. The CFIA and APHIS have implemented the Plant Protection Act and subsequently several Plant Protection Policy Directives (APHIS 2015; CFIA 2015). Nurseries in quarantine must be inspected annually for *P. ramorum*. Pre-shipment inspections of plants are required before national movement. Eradication efforts are initiated if the pathogen is detected during the inspection process, which includes removal and destruction of the infected hosts, nursery stock, soil, wood packaging materials, and firewood.

For the E.U. community, following the first description of *P. ramorum* by Werres et al. (2001), the European and Mediterranean Plant Protection Organization (EPPO) listed *P. ramorum* on their quarantine organisms list. The E.U. Commission took provisional emergency phytosanitary measures against the introduction and spread within the E.U. These measures were implemented in 2002 and were revised in 2004 and 2007 (Redlin et al. 2014). In addition to recommendations for import or movement of host plants, each E.U.-member state must conduct an annual survey for *P. ramorum* within its territory. Monitoring must be carried out in nurseries, parks, and woodlands. During 2004–07, a European research project (RAPRA) was carried out to develop a comprehensive PRA and its last review was produced in 2009 (Sansford et al. 2009).

Canadian Forest Service research scientists have either significantly contributed to or authored all of the national risk analyses for *P. ramorum*, coordinated through the Plant Health Risk Assessment (PHRA) Unit, Plant Health Science Division, CFIA. Although these PRAs are not published in peer-reviewed journals, they are detailed, often lengthy, science-based evaluations that analyze all the risks and synthesize the substantiating data into a format useful to decision makers. Using "low," "medium," or "high" values, the summary at the beginning of each PRA predicts both the likelihood of introduction of *P. ramorum* to Canada and the consequences of introduction. The Canadian PRA also used these values to rate the overall risk and the level of uncertainty associated with it (Fig. 2).

In the first Canadian PRA for *P. ramorum* (Cree et al. 2001), the likelihood of introduction was rated "medium" because the information on the pathogen was then scarce and the list of known hosts was small. The consequences of introduction were rated "high" because many of the known hosts occurred in Canada as prominent horticultural and forest species, and under laboratory conditions, they could

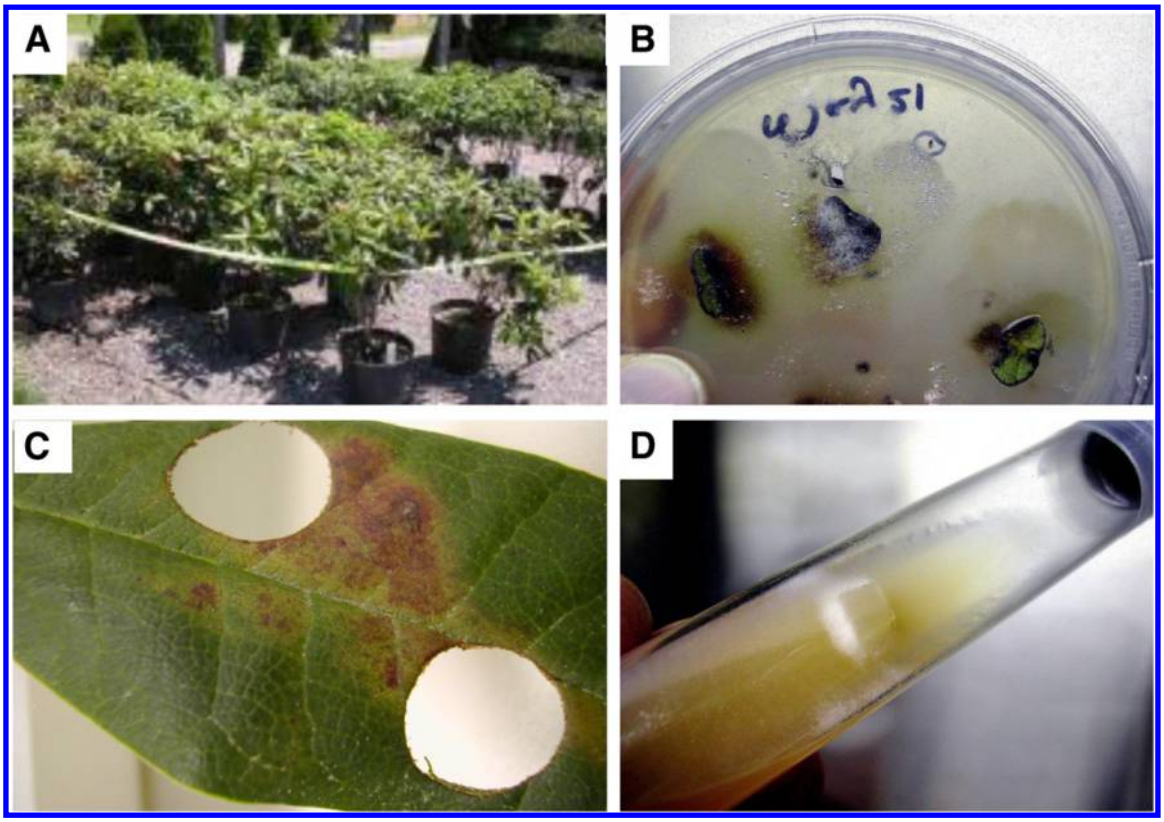

Fig. 1. This photo block tells the story of the first detection of *Phytophthora ramorum* in Canada in 2003 on imported plants at a BC nursery site. The detection resulted from trace forward activities by the USDA. The leaf and cultures are photos of the original material. **A,** First positive detection of *P. ramorum* in Canada was found in imported *Rhododendron* sp. cv. Vulcan plants. **B,** The positive leaf displayed characteristic symptoms of *P. ramorum* infection such as reddish-brown leaf spots with diffuse margins. **C,** Excised leaf disks from leaves similar to that shown in B plated onto PARP medium. The pathogen grew well on PARP and sporangia and chlamydospores were visible by 7 days after incubation. The organism was identified by comparative morphology to a reference strain of *P. ramorum* and morphometrically compared with the species described by Werres et al. (2001). **D,** The morphological identification was performed on a purified culture and subsequently confirmed by a positive PCR reaction of mycelial DNA using the Phyto 1 and Phyto 4 primers and protocol (Garbelotto et al. 2002). All photos are from S. C. Brière, CFIA.

be infected. Potential economic impact was rated "medium" for most host species, but "high" for some economically valuable confirmed hosts such as *Quercus* (oak), *Rhododendron*, and *Vaccinium* (blueberry), even though the susceptibility level was unknown for most of these species. The overall risk rating was deemed "medium" while the level of uncertainty was rated "high," mainly due to lack of information on this newly discovered pathogen. Shortly thereafter, a report summarized the economic impact of *P. ramorum* in Canada, including on plant exports and costs associated with national surveys and diagnostics (Allen et al. 2003).

In April 2004, the risks posed by importation of a single host genus, *Rosa*, were assessed by CFIA and CFS (Allen and Cree 2004), after plants of *Rosa gymnocarpa* Nutt. with foliar and petiole lesions caused by *P. ramorum* were discovered in Sonoma County, California, shortly before nearly 2.2 million rose plants were scheduled for import into Canada from the U.S. After further investigation, the risk of introduction was deemed low. A checklist for assessing roses from specified jurisdictions was devised and further safeguards were also recommended, and thus the roses were permitted entry into Canada.

An extensive update of the PRA was published by CFS authors in 2006 (Rioux et al. 2006). At this moment, the pathogen had been detected, but subsequently eradicated in nurseries in BC in both 2003 and 2004. Because of the degree of research already undertaken by the scientific community, the level of uncertainty of this PRA was reduced to "medium" and areas of research required to further reduce uncertainty were also identified, including determining the potential of *P. ramorum* to infect different plant species common in eastern Canada.

The current PRA (Kristjansson and Miller 2009) rated the likelihood of introduction of *P. ramorum* to Canada as "high" based on factors including the high volumes of internationally traded live plant material, the likelihood being that some is potentially infected at source, and the availability of susceptible hosts at ports of entry. The climate-based predictive maps included in this PRA indicated that south-coastal BC has the highest suitability for the establishment of *P. ramorum*. However, for other regions, not all models concurred, some suggesting no risk to eastern Canada while others indicated that areas in south central BC, southern Ontario, and Quebec, Nova Scotia, PEI, New Brunswick, and southern Newfoundland were at low to moderate risk. As the body of knowledge on this pathogen accumulated over time, the level of uncertainty was rated "low" in this last Canadian PRA.

Indirect economic losses due to domestic phytosanitary actions taken between 2003 and 2006 were estimated at $3 million for plant destruction and $500,000 for sanitation and disposal. In 2010, compensation payments to nurseries had reached $21.2 million (Canada Gazette 2010). Future consideration of indirect economic impact to trade should also be considered if *P. ramorum* ever became established in forested environments. For instance, although kiln drying is thought to eliminate the pathogen in lumber, there could be potential impacts to log exports, valued in Canada at $580 million in 2012 (Niquidet 2012).

Risk to conifer species. On 3 March 2007, the North American Plant Protection Organization (NAPPO) sponsored a discussion panel to review the state of scientific knowledge regarding the risks posed by *P. ramorum* to conifers and the potential for the pathogen to be transported with conifer forest products moving in international trade (Callan et al. 2008). It was led by CFS and CFIA experts, and attended by over 100 participants, including researchers and forest managers from several countries. At the time, only a few conifers were proven hosts. Reviews were presented by leading scientists in the field of *P. ramorum*, followed by a general discussion on the gaps in scientific knowledge. The panel agreed that the risks of spread of *P. ramorum* by trade in conifer commodities such as lumber and logs was extremely low, compared with other pathways such as infected nursery stock, soils, or leaves and branches of host plants known to support high levels of sporulation.

Soon after the latest revision of the Canadian PRA was completed in 2009, new reports of *P. ramorum* spreading to plantation-grown Japanese larch, *Larix kaempferi* (Lamb.) Carr., causing extensive defoliation, dieback, and mortality were reported from the United Kingdom (Brasier and Webber 2010). The shift of *P. ramorum* to larch species was a new and alarming development in the epidemiology of the pathogen (Jones 2014). At about the same time, artificial inoculations of the foliage of various tree species common in eastern Canada revealed that tamarack, also called eastern larch (*L. laricina* [Du Roi] K. Koch), presented some level of susceptibility (Jinek et al. 2009) and this was even more prominent when the stem was inoculated (Simard et al. 2010). Preliminary evidence suggests that although there is a small likelihood of *P. ramorum* penetrating the sapwood of larch, this is likely to be infrequent and only in the outermost layers of wood. Therefore, logs harvested from infected larch can be used in the wood production chain if appropriate biosecurity protocols are applied (Webber et al. 2010b).

Epidemic spread of *P. ramorum* in the western U.S. and the U.K. has only occurred in wet, cool coastal areas where the presence of both susceptible canker hosts and foliar hosts supporting high levels of sporulation coincides with a favorable environment. Epidemiological studies have revealed a requirement for high inoculum levels in order for the pathogen to cause cankers on susceptible host trees (Davidson et al. 2005; Webber et al. 2010a). In 2013, CFIA and CFS jointly authored a report to assess whether, if introduced, *P. ramorum* would pose a similar threat to native and introduced larch species in Canada (Deng and Callan 2013). In Canada, long and cold winters are considered limiting factors for the establishment and spread of *P. ramorum*. The three native larch species, alpine larch (*Larix lyallii* Parl.), western larch (*L. occidentalis* Nuttall), and tamarack (*L. laricina*) are largely distributed outside of the at-risk areas in Canada predicted by various models. Tamarack also grows in southern parts of Ontario and Quebec and the Maritime Provinces where *P. ramorum* may be likely to establish. Results of a recent inoculation study indicated that tamarack was somewhat susceptible but had low levels of sporulation on wounded leaves (Jinek et al. 2011). European (*L. decidua* Mill.) and Japanese larch and their hybrids are the main exotic larches grown in eastern Canada, mainly for landscape purposes, but also in limited commercial plantations in Quebec and Newfoundland where they are far more productive than their native counterparts (Stipanicic 1999; Vallee and Stipanicic 1983). Millions of these larch seedlings have been planted in Quebec and Newfoundland (A. Deschaies, pers. comm. in Deng and Callan 2013; English, pers. comm. in Deng and Callan 2013). As Japanese and European larches are both proven canker and foliar hosts, climatic suitability in eastern Canada becomes the critical factor in the assessment of potential risks of *P. ramorum* to these larch species

PRA Year	Location	Likeliness of introduction	Consequences of introduction	Overall risk rating	Assessment uncertainty level
2001	All of Canada	Medium	High	Medium	High
2006	BC	High	High	High	Medium
	Eastern Canada	High	Medium	Medium	Medium
2009	South coastal BC		Medium		
	South Ontario, Quebec, Inland BC		Low		
	Rest of Canada		Negligible		

Fig. 2. Summary of *Phytophthora ramorum* pest risk assessments for Canada.

and their hybrids grown in the region. Analyses of multiple models suggest that *P. ramorum* would be unlikely to establish and spread in the areas in Quebec where exotic larches are grown commercially (Deng and Callan 2013). However, the pathogen may be able to establish in warmer parts of the Maritime Provinces and southern parts of Ontario, though the likelihood of epidemic spread of the pathogen in these areas appear to be relatively low.

In eastern Canada, damage from the establishment of *P. ramorum* might also likely be limited by seasonal defoliation. As larch trees naturally shed all foliage every fall, the disease cycle would thus begin each spring primarily from overwintered chlamydospores in litter on the ground and gradually spread from understory foliar hosts to taller trees as increasing amounts of inoculum become available, with disease progression stopping each year by winter. Thus, Deng and Callan (2013) concluded it was unlikely that the inoculum of *P. ramorum* would increase to levels high enough to cause epidemic outbreaks on introduced larches during the short growing season in eastern Canada, especially in areas where the larch species are not grown in dense plantations. Newfoundland, with its relatively large number of Japanese larches grown in plantations, might be slightly more at risk. If introduced there, *P. ramorum* might establish, persist, and spread in exotic larch plantations, with damage possibly accumulating to measurable levels over years, similar to levels caused by other larch needle casts and blights already established in the region. It is unlikely, however, that *P. ramorum* would cause the level of damage on larches as seen in the U.K.

In summary, it appears that neither native nor exotic larch would support or accumulate sufficient levels of prolific sporulation to cause extensive mortality of larches and other conifers under the colder and less favorable Canadian climatic conditions, despite the availability in some areas of susceptible species which could serve as both canker and foliar hosts. The risk rankings for *P. ramorum* in eastern Canada, including southern Ontario and Newfoundland, remain low as concluded in the 2009 PRA, and no further updating to that document was considered following the unexpected discovery of *P. ramorum* in Japanese larch in the U.K.

Modeling to map the risk of *P. ramorum* spread in Canada. Researchers at the Natural Resources Canada–Canadian Forest Service–Great Lakes Forestry Centre (NRCan-CFS-GLFC) have developed models to determine the risk of *P. ramorum* spreading in Canada. Several approaches have been used to identify the climatic tolerances of *P. ramorum* (Browning et al. 2008; DEFRA 2004; Englander et al. 2006; Garbelotto et al. 2003; Tooley et al. 2009; Werres et al. 2001). These findings, and others, have been used in ecophysiological models to simulate the growth and survival of *P. ramorum* both in the United States (Venette and Cohen 2006) and globally (Ireland et al. 2013).

Another approach for estimating climatic suitability is to summarize the climatic conditions at locations where a species is known to occur in natural settings. A variety of methods have been developed for this purpose, ranging from basic statistical summaries to sophisticated machine learning techniques (Elith et al. 2006). The application of these methods to invasive alien species presents a number of unique challenges (Broennimann et al. 2007; Elith et al. 2010; Medley 2010; Venette and Cohen 2006). Despite these caveats, distribution models have played a useful role in identifying climatically suitable locations for the introduction and spread of a variety of invasive species (Bomford et al. 2009; Broennimann et al. 2007).

Here we present climatic suitability maps for *P. ramorum* (Fig. 3) using updated distribution data from North America and Europe (http://oakmapper.org; Kelly and Tuxen 2003; Kelly et al. 2004; European and Mediterranean Plant Protection Organization [EPPO]). All data were for locations where *P. ramorum* had become established on vegetation outside the plant nursery setting. Gridded climate data for North America (McKenney et al. 2011) and Europe (Hijmans et al. 2005) were assembled for the 1971 to 2000 period for 19 bioclimatic variables (see McKenney et al. 2011 for listing). Future grids of the same climate variables were obtained for the 2041 to 2070 period for an ensemble of four general circulation models (GCMs; see Price et al. 2011 for details) and the RCP 8.5 emissions scenario (van Vurren et al. 2011). Climate suitability was modeled using Maxent (Elith et al. 2006, 2010; Phillips et al. 2006), a modern machine learning approach that predicts the distribution of an organism by finding the distribution of maximum entropy (i.e., the closest to uniform) that respects a set of constraints derived from the occurrence locations.

Figure 3A shows the probability of occurrence of *P. ramorum* in Europe based on a Maxent model using only European occurrence locations. The most influential climate variables in this model distinguish maritime and continental climates; specifically, *P. ramorum* was positively associated with locations that had a small annual temperature range and consistent precipitation levels throughout the year. When this model was projected onto North America (Fig. 3B), the west coast of Canada was identified as highly suitable for *P. ramorum*.

Figure 3C shows the probability of occurrence of *P. ramorum* in North America based on a Maxent model using only North American occurrence locations. The strongest relationships were associated with temperature and precipitation seasonality. When this model was projected onto Europe (Fig. 3D), coastal areas around the Mediterranean Sea were identified as climatically suitable for *P. ramorum*. Interestingly, there was very little overlap between the climatically suitable areas identified using the two data sources; the model developed using the North American data did not predict the occurrence of *P. ramorum* in Europe and vice versa. This may reflect the significant genotypic and phenotypic differences that exist between *P. ramorum* populations in North America and Europe (Ivors et al. 2006). Alternatively, it may be that *P. ramorum* populations on one or both continents have not yet expanded to fully occupy their potential climate niches, supporting the notion that incomplete occurrence data associated with rapidly expanding invasive species can limit the accuracy of species distribution models.

Figure 3E shows the probability of occurrence of *P. ramorum* in North America based on a Maxent model using both North American and European occurrence data. The result identifies much of the west coast of North America as having suitable climate for *P. ramorum*. When this model is projected onto climate grids for the 2041 to 2070 period (Fig. 3F), much of the west coast remains climatically suitable and newly habitable areas emerge along the southern coast of Alaska.

Our findings are similar to those reported from ecophysiological models (Ireland et al. 2013; Venette and Cohen 2006) with respect to the identification of the west coast of North America as being highly suitable for *P. ramorum*. However, the ecophysiological models also identify significant portions of the eastern United States and a small portion of southeastern Canada as suitable. Much of this discrepancy is due to uncertainty around moisture constraints on *P. ramorum* survival and growth. Although outbreaks have occurred only in coastal areas with significant rainfall, both of the ecophysiological studies set relatively low limits on moisture requirements for growth (i.e., soil moisture at 20 to 40% of field capacity); this parameter setting has little direct support from laboratory studies, but has been shown to significantly impact model predictions (Venette and Cohen 2006). Alternatively, the distribution data collected to date may simply not reflect the full climatic niche of this species. This issue has important implications for the amount of area at risk of invasion by *P. ramorum* in North America.

Canadian Research Activities

To generate information upon which to base regulatory decisions, research was undertaken in several Canadian laboratories on the diagnostics, biology, and management of *P. ramorum*. Collaboration with researchers in the U.S. and Europe continues to this day. The following are an overview and highlights of the major contributions by Canadian scientists on the *P. ramorum* pathosystem.

Molecular detection, diagnostics, and population studies. Canadian government and academic laboratories have intensively worked on the development of detection and genotyping methods of *P. ramorum* since its description as a new species in 2001 (Werres et al. 2001). In the early 2000s, regulations were put in place to detect potential incursions of *P. ramorum* into Canada. Research teams at

NRCan, CFIA, and AAFC worked on the development of methods for detecting the pathogen, so when *P. ramorum* was discovered for the first time in Canada in 2003, the CFIA was able to respond rapidly to inspection and survey needs by using these molecular assays. The following sections give an overview of the studies leading to those developments.

Detection/diagnostic research in Canada. One of the best ways to prevent the establishment of any invasive species is to detect it as early as possible. The CFIA lab in Ottawa has done much research into this issue. In the early 2000s, a culture and ELISA assay followed by PCR was the commonly used procedure. This method, however, was limited as it detected only the *Phytophthora* genus, often generating false positives as also observed when the same method was used in the U.S. (Osterbauer and Trippe 2005). To solve this problem, new markers, using multiple gene regions to design redundancy, were developed to help increase the specificity and sensitivity for the detection of *P. ramorum* (Bilodeau et al. 2007b). The three assays developed by Bilodeau et al. (2007b) combined with selective media are currently being used by the CFIA for the detection of this pathogen and they are also exploited elsewhere (Hughes et al. 2006). The method of Bilodeau et al. (2007b) was also developed to be utilized in a multiplex assay with an internal control for the plant and *Phytophthora* spp. (Bilodeau et al. 2009). To improve the accuracy of the markers to detect both the genus and *P. ramorum*, without amplification of the closely related genus *Pythium*, a multiplex assay was developed based on differences in the mitochondrial gene for two regions, *atp9-nad9* and *trnM* (Bilodeau et al. 2014b). In this assay, a set of genus-specific primers and probes was developed with multiple species-specific probes, including one for *P. ramorum*.

The assays developed to detect other *Phytophthora* spp. (Chen et al. 2013; Miles et al. 2014) provide simple procedures easily adaptable to miniaturization to identify species in environmental samples without the requirement for isolation and culturing, adding to the toolbox to prevent and manage plant diseases caused by *Phytophthora*. Moreover, using genome sequence information, a Taqman assay on Cluster62, a protein without any known function, was developed in combination with other pathogen assays allowing in the end the rapid and reliable detection of 10 of the most unwanted

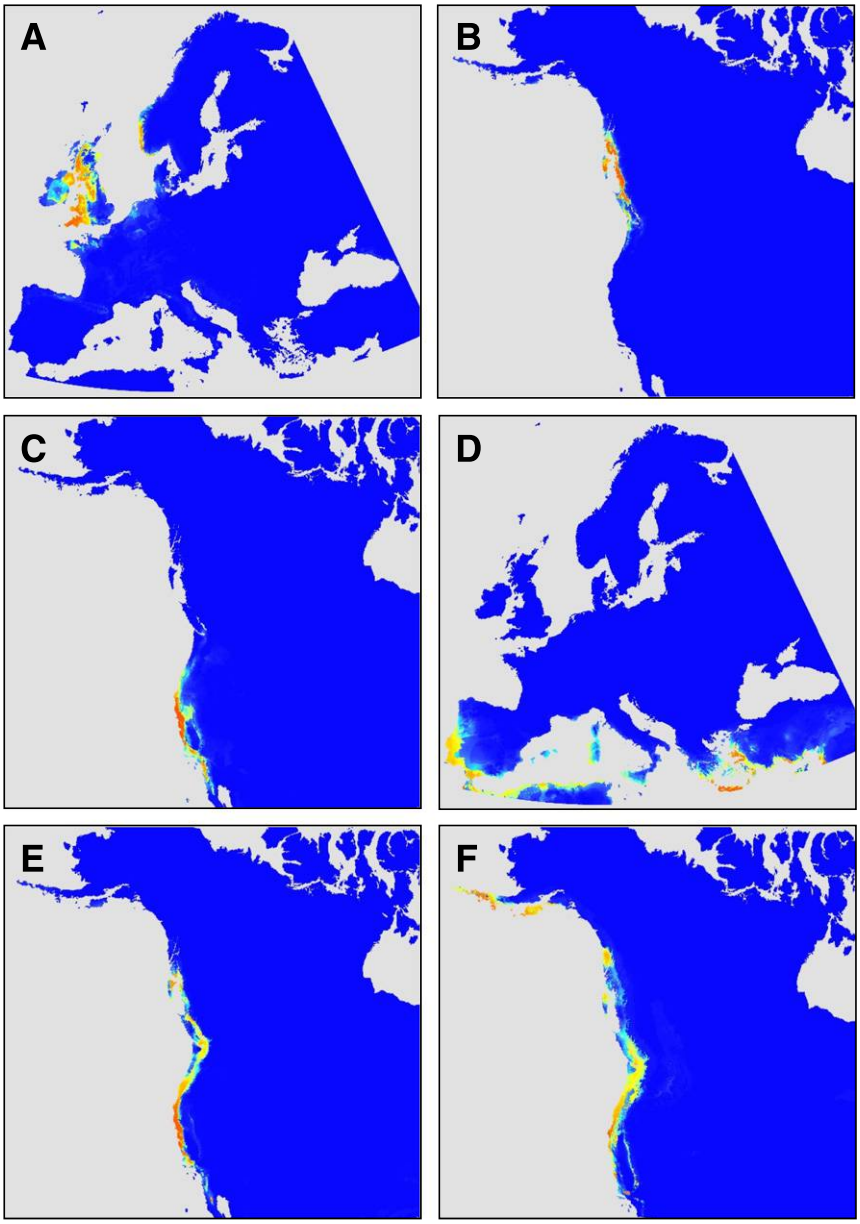

Fig. 3. Maxent distribution models showing climatic suitability for sudden oak death (SOD) in Europe, based on European occurrence locations (**A**); in North America, based on European occurrence locations (**B**); in North America, based on North American occurrence locations (**C**); in Europe, based on North American occurrence locations (**D**); in North America, based on both European and North American occurrence locations (**E**); in and North America, under future climate predictions (2041-2070, RCP 8.5, ensemble of four GCMs), based on both European and North American occurrence locations (**F**).

alien forest pathogens, including *P. ramorum*, in Canada (Lamarche et al. 2015).

Genotyping. Genotyping allows identification of variants within species, providing for instance crucial information about the sources of outbreaks. Several markers have been developed to genotype and identify *P. ramorum* clonal lineages (Gagnon et al. 2014). Genotypes of three lineages present in Canada (NA1, NA2, and EU1) have been examined using PCR-RFLP (Elliott et al. 2009b) and their phenotypes for aggressiveness and growth rate on detached leaves (Elliott et al. 2011). Microsatellite markers were also used to genotype Canadian isolates in samples collected from 2003 to 2008, which resulted in the frequent identification of isolates belonging to the NA2 lineage (Goss et al. 2010). Following this finding, microsatellite markers that are polymorphic within the NA2 lineage were developed using a de novo assembly of the genome of the *P. ramorum* NA2 lineage (Bilodeau et al. 2014a; Gagnon et al. 2017).

However, one drawback of microsatellite markers is that they usually cannot be used for direct testing of field material without prior DNA extraction from cultures and molecular validation. To address this issue, allele-specific oligonucleotide (ASO)-PCR assays were developed to differentiate the *P. ramorum* lineages using real-time PCR (Bilodeau et al. 2007a; Gagnon et al. 2014). Combining these assays, it is now possible to identify all four lineages directly from infected tissues without the need for culturing the pathogen. All Canadian isolates discovered and isolated since 2003 were genotyped using ASO-PCR (Fig. 4).

By scanning genomes, it is possible to identify patterns of polymorphisms such as single nucleotide polymorphisms (SNPs) (Bilodeau 2008; Bilodeau et al. 2006). As part of the Tree Aggressors Identification using Genomic Approaches (TAIGA, http://taigaforesthealth.com) project, the genomes of 92 isolates of *P. ramorum* belonging to the four known lineages were sequenced and de novo assemblies were performed for each lineage. Genome-wide patterns of diversity in the four lineages of *P. ramorum* were studied, including analysis of SNPs (Dale et al. 2013), and this resulted in the identification of a large number of polymorphisms and generated a powerful set of tools for both population genomics analyses and monitoring of the pathogen. These DNA-based tools will contribute to the available genomic toolbox to assess the genetic diversity of these pathogens, from the species to the intralineage level.

Other molecular tools in development in Canadian laboratories. With the new era of next generation sequencing (NGS), metagenomics is now possible for detection of organisms directly from environmental samples. Bilodeau et al. (2016) recently conducted a proof of concept in metagenomics to detect pathogens from spore traps. The region of *atp9-nad9* (Bilodeau et al. 2014b) and ITS specific for oomycetes were used for detection of *P. ramorum* in samples using labeled primers and Ion Torrent personal genome machine (PGM) technology (Bilodeau, unpublished).

Robideau et al. (2014) generated phylogenies of oomycetes using flagellar genes, showing that there are some highly conserved and highly variable genes in the flagellar apparatus. Exploiting the power of antibodies on microchips, this technique could have great value when testing water bodies for early detection of invasive *Phytophthora* spp. To improve sample preparation for selection of specific spore material for eventual DNA extraction from field material, detection, and metagenomics, *P. ramorum* propagules and DNA were used to validate the method (Geissler et al. 2011). The qPCR assay TaqMan on *atp9-nad9* (Bilodeau et al. 2014b) was then used for evaluation of the chips. Those are only few new molecular methods and tools now in advancement. With technology progressing and availability of NGS, new tools, implementation, and reformatting of developed technologies are in progress.

Phenotypic differences. Researchers at the NRCan-CFS-Pacific Forestry Centre (PFC) laboratory in Victoria, BC, and at the CFIA Sidney laboratory have studied a range of phenotypic characters of *P. ramorum*. Significant differences exist between the NA1, NA2, EU1, and EU2 lineages of *P. ramorum*, such as growth rate, colony stability, and extreme temperature limits for growth and aggressiveness (Brasier et al. 2006; Elliott et al. 2010; Manter et al. 2010; Webber et al. 2014). Phenotypic instability has been reported in the NA1 lineage of *P. ramorum*. For instance, the so-called wild type (*wt*) isolates present a uniform culture morphology and low variability in growth rate but degenerate upon subculturing to become morphologically irregular and more variable in growth rate and pathogenicity (Brasier et al. 2006; Elliott et al. 2011). It has been suggested that subculturing NA1 rapidly causes culture instability and loss of aggressiveness, and passages through the host are particularly necessary with this lineage to restore its original aggressive state.

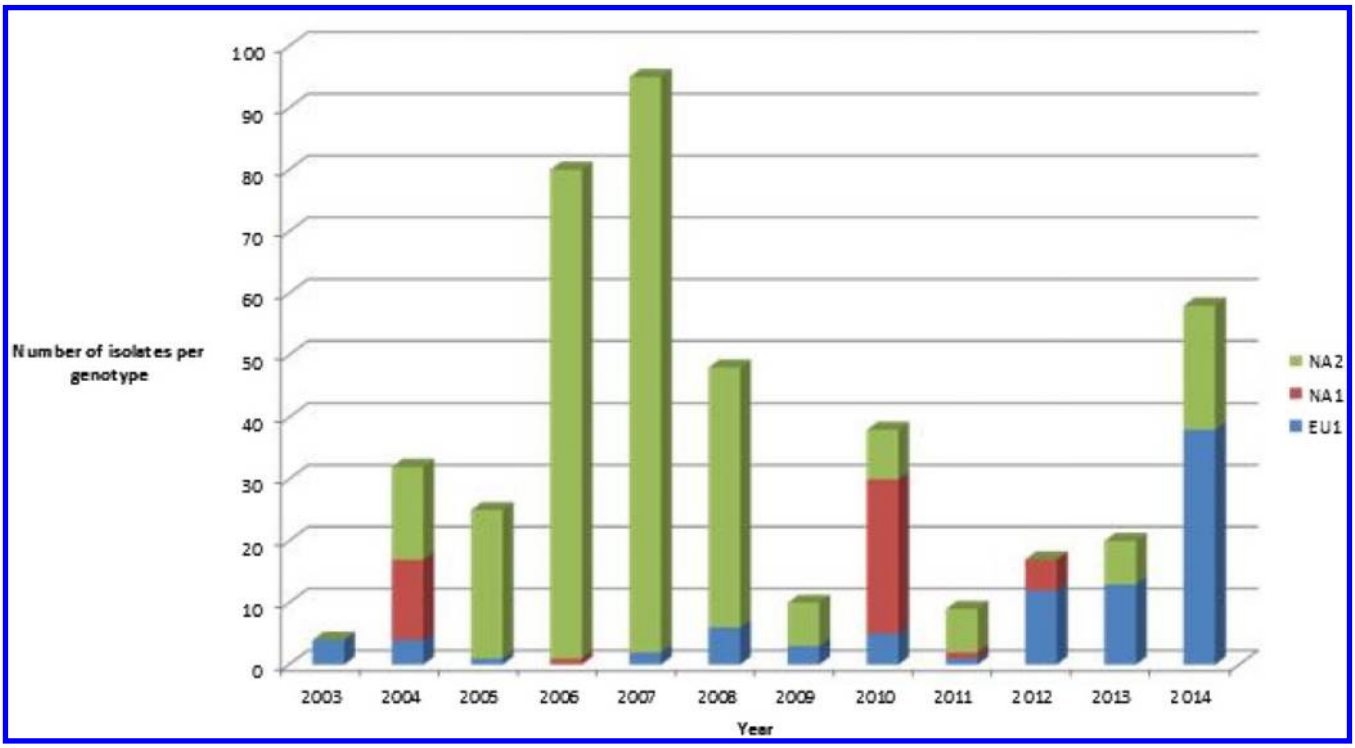

Fig. 4. Number of Canadian isolates genotyped per year using allele specific oligonucleotide (ASO)-PCR (Bilodeau, unpublished).

To test this phenomenon, slow growing and less aggressive non-wildtype (*nwt*) isolates of *P. ramorum* were compared with *wt* isolates having normal growth and aggressiveness by successive reisolation from host material.

In both *wt* and *nwt* groups, there were significant differences in lesion size on detached rhododendron leaves between the original culture and the first reisolation (Elliott et al. 2010). After reisolation from the host, *nwt* isolates were still less aggressive than *wt* isolates (Fig. 5). Along with lower aggressiveness on rhododendron leaves, *nwt* isolates produced fewer chlamydospores in V8 agar than did *wt* isolates and they were more sensitive to temperature extremes.

To understand the cause of these phenotypic differences in *wt* and *nwt* isolates, a study by Kasuga et al. (2012) attributed this phenomenon to epigenetic changes rather than to conventional mechanisms. Kasuga et al. (2016) also showed that *nwt* isolates from oak (*Quercus* spp.) and Lawson cypress (*Chamaecyparis lawsoniana*) bark cankers have chromosomal abnormalities absent in *wt* isolates. These authors postulate that the host defense mechanisms cause chromosomal damage in these isolates.

Infection process and host defense mechanisms. *Infection process.* The infection process of *P. ramorum* was studied by researchers at the NRCan-CFS-Laurentian Forestry Centre (LFC). In a study of the host range of *P. ramorum* on Canadian forest tree species common in eastern Canada (*Abies balsamea* L. [Mill.] [balsam fir], *Acer saccharum* Marsh. [sugar maple], *Betula alleghaniensis* Britt. [yellow birch], *Fraxinus americana* L. [white ash], *Larix laricina* [Du Roi] K. Koch [tamarack], and *Quercus rubra* L. [red oak]), using artificial inoculations, young leaves were found to be more susceptible to *P. ramorum* infection than older ones, particularly with species such as white ash and red oak (Jinek et al. 2011). Similar findings on foliage have been published elsewhere (Balci et al. 2008; Denman et al. 2005; Hansen et al. 2005). Studies conducted by the CFS showed that rhododendron leaf colonization occurs shortly after inoculation with intercellular hyphal growth. In more advanced infection stages with susceptible species, intracellular growth also occur, particularly when necrosis is present. The veins are then invaded, leading to the colonization of the shoots (Fig. 6A and B).

In addition, inoculations of the stem of 2- to 3-year-old seedlings of the tree species described above were compared with and without wounding using colonized agar plugs. It was clear that wounding is necessary to induce the appearance of symptoms (Rioux, unpublished results). Zoospores are able to penetrate intact bark of mature trees, but this is more common on trees with thin bark, such as *F. sylvatica* (Brown et al. 2006).

The presence of *P. ramorum* within xylem elements and direct penetration of pit membranes in the stem of balsam fir and tamarack has been frequently observed in research carried out by CFS (Fig. 6C), obviously implying that the pathogen produces the right enzymes, such as pectin esterases reported for other *Phytophthora* spp. (Mingora et al. 2014).

Besides these considerations, tree phenology could also influence the outcome of host-*P. ramorum* interactions. Dodd et al. (2008) reported that oak trees are more susceptible to infection in the spring and they have associated this fact with the intense activity of the cambium and particularly the production of large vessels. This same phenomenon was observed during artificial inoculation assays. When the plants were less active at the end of the growing season, most inoculations failed to induce symptom development (Rioux, unpublished results).

Host defense mechanisms. Researchers at the NRCan-CFS-LFC are currently working on the defense mechanisms of several tree species that have been artificially inoculated with *P. ramorum*. Even though *P. ramorum* can successfully infect a wide host range, artificial inoculations in favorable conditions have revealed that some tolerance or resistance to this pathogen occurs (Grünwald et al. 2008; Tooley et al. 2004). However, little is known about the mechanisms that help limit or halt colonization by *P. ramorum* or any other *Phytophthora* spp. (Oßwald et al. 2014). Cell wall modifications, such as the accumulation of callose and the production of phytoalexines, have been reported in some plant species.

Tyloses in red oak and white ash and the formation of gels in species such as sugar maple and yellow birch were observed following stem inoculations with *P. ramorum* (Fig. 7A). These occluding structures were associated with a reduction in hydraulic conductivity, as was seen in research on tanoak (Collins et al. 2009). Several of these structures accumulate phenols that may render them more resistant to pathogen attacks. Canadian investigations have revealed the presence of phenols in these structures in other host-pathogen relationship (Rioux and Ouellette 1989; Rioux et al. 1998).

Following stem inoculations with *P. ramorum*, the formation of various tissues that are associated with the compartmentalization

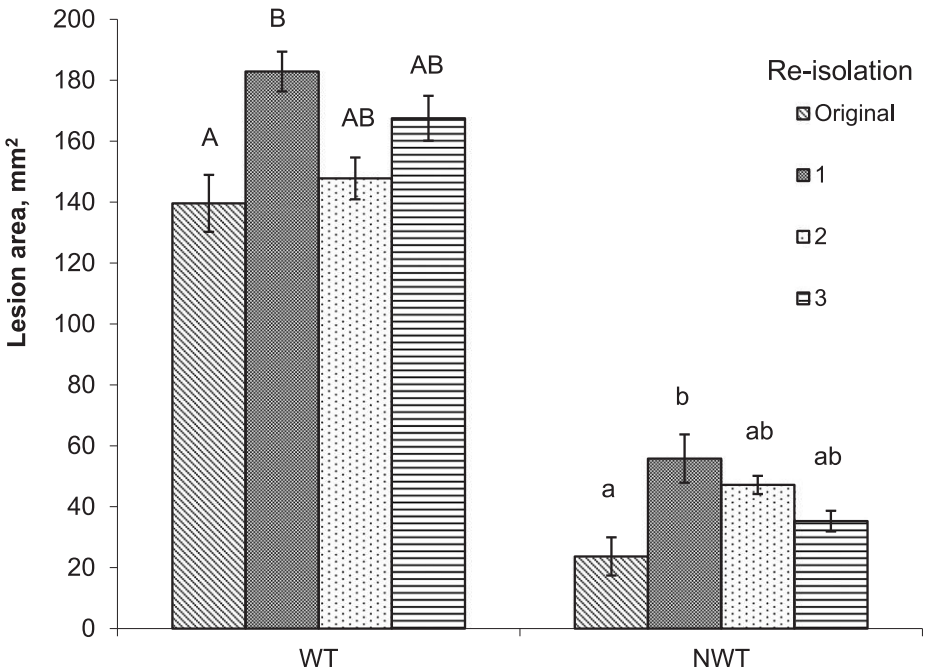

Fig. 5. Differences in lesion size induced by wild type (*wt*) and non-wildtype (*nwt*) isolates of *Phytophthora ramorum* on Rhododendron 'Cunningham's White' leaves. Significant differences were found between *wt* and *nwt* isolates for all reisolations, and between reisolations within *wt* and *nwt* only for the original culture and the first reisolation. Groups with the same letter are not significantly different (ANOVA, SNK multiple comparisons, $P < 0.001$).

concept was regularly observed, as proposed for either the xylem (Shigo 1984) or the bark (Biggs 1992; Shigo 1984). For instance, in sugar maple, a new periderm was formed in the bark and the invaded xylem was usually quite limited (Fig. 7B), thanks in part to the accumulation of phenolic compounds around the invaded wood (Fig. 7C). Accumulation of phenols was also observed in inoculated roots and leaves generally associated with zones that seemed to limit the colonization of the pathogen (Rioux, unpublished results).

Deposition of callose has been detected in greater intensity in the bark of tanoak infected by *P. ramorum* than in uninfected controls (Giesbrecht et al. 2011). Callose has often been associated with defense against pathogens, particularly as a constituent of papillae, which are localized deposits on the internal cell walls (Aist 1976). Microscopic examinations by CFS' scientists have shown the occasional presence of papillae in inoculated leaves of some of the tree species studied. Using a monoclonal antibody specific for β-1,3-glucans, it was possible to confirm the presence of callose in balsam fir needles, even though at times such papillae were apparently not strong enough to prevent pathogen penetration (Fig. 7D).

Canadian host susceptibility. Scientists in western Canada (NRCan-CFS-PFC) and eastern Canada (NRCan-CFS-LFC) are working on determining the potential host range of *P. ramorum* should it become established in Canada. *P. ramorum* can infect numerous plant species and this large host range continues to expand at a steady rate. The CFIA lists around 130 hosts (CFIA 2015) on which Koch's postulates have been confirmed. This list contains five groups of

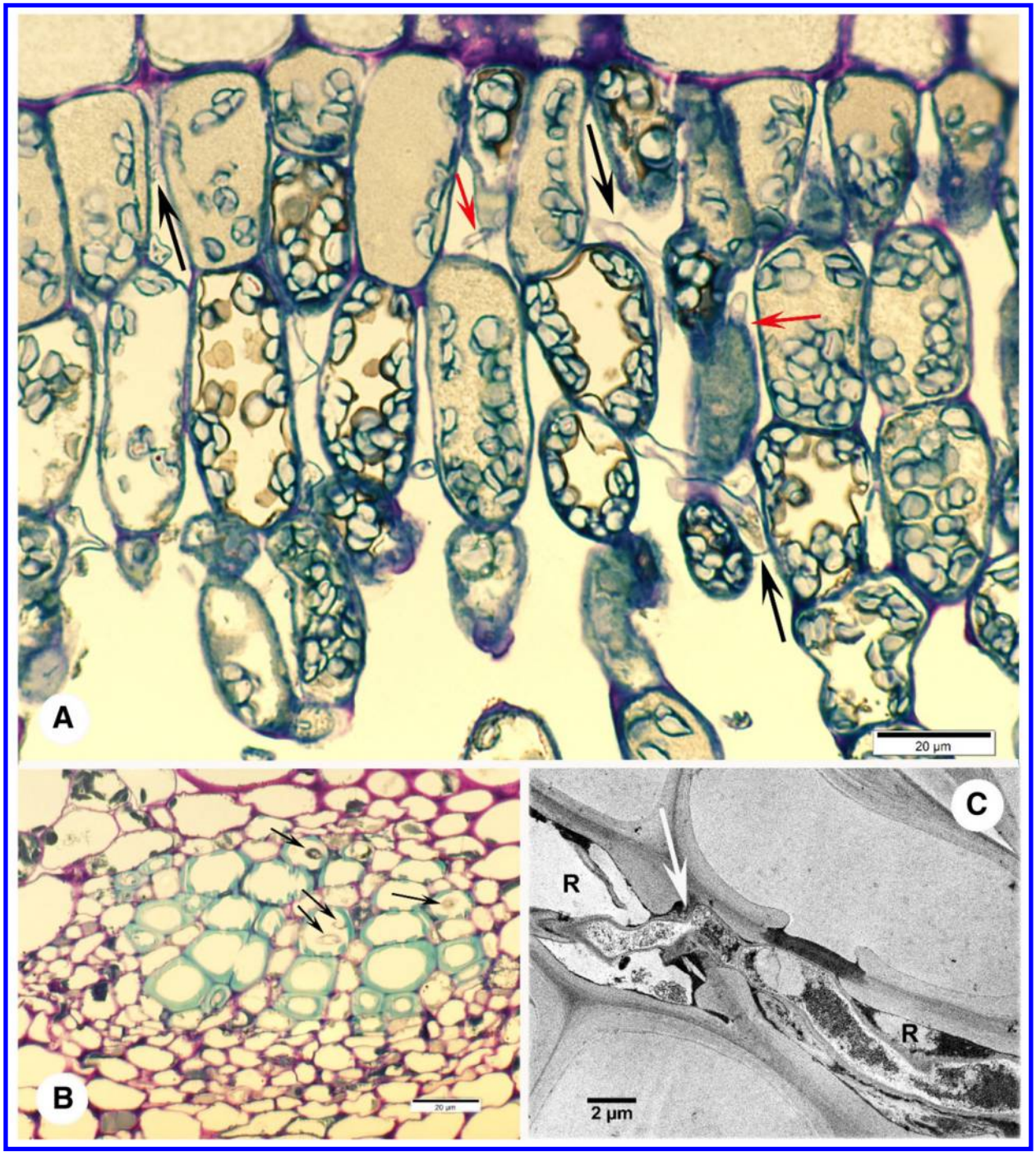

Fig. 6. A, *Phytophthora ramorum* hyphae are seen intercellularly (black arrows) among these palisade parenchyma of a rhododendron leaf. Some hyphae also penetrate some of the host cells (red arrows). Numerous chloroplasts are obvious within parenchyma cells. **B,** Pathogen cells (arrows) colonize the xylem (walls in blue) of a major vein in a lilac leaf. **C,** A hypha crosses the pit membrane (arrow) between two ray cells (R).

hosts particularly susceptible to *P. ramorum* that are regulated at the genus level.

Using adequate containment facilities, it is possible, and generally necessary, to inoculate common plant species in areas that are free of the disease to help assess the risk of establishment of *P. ramorum*. It is not unusual to later find during surveys that such "experimental" hosts can indeed be naturally infected by *P. ramorum*. For instance, red oak was first identified as susceptible to *P. ramorum* following artificial inoculations (Rizzo et al. 2002; Tooley and Kyde 2003) before being found naturally infected in the Netherlands (Steeghs and de Gruyter 2005).

CFS researchers inoculated the foliage of tree species common in eastern Canada (Jinek et al. 2011). The degree of leaf necrosis was particularly high on white ash and yellow birch, while on conifers it was more obvious on balsam fir than on tamarack. The same species were stem-inoculated and more damage occurred on balsam fir, tamarack, and red oak than on other species (Simard et al. 2010). Approximately 25% of the conifers died above the inoculation point while bark necrosis was the main symptom observed on red oak. Penetration of the pathogen through the roots of red oak and balsam fir was also examined (Tsae et al. 2012). The roots of red oak and balsam fir were less susceptible to infection by *P. ramorum* than those of a rhododendron used as a control.

In British Columbia, detached leaves of plants commonly found in forests or ornamental landscapes were inoculated with different isolates of three lineages of *P. ramorum* (Elliott et al. 2011). Not surprisingly, *Camellia japonica* 'Pink Diddy' was particularly susceptible to *P. ramorum* while the degree of necrosis tended to decline in the other species tested, namely Pacific madrone (*Arbutus menziesii*), salal (*Gaultheria shallon*), and Oregon grape (*Mahonia nervosa*), in decreasing order of susceptibility. While the isolates from NA2 and EU1 lineages were more aggressive than those from the NA1 group on the rhododendron tested, no significant differences among isolates were disclosed when the other species were inoculated with *P. ramorum*.

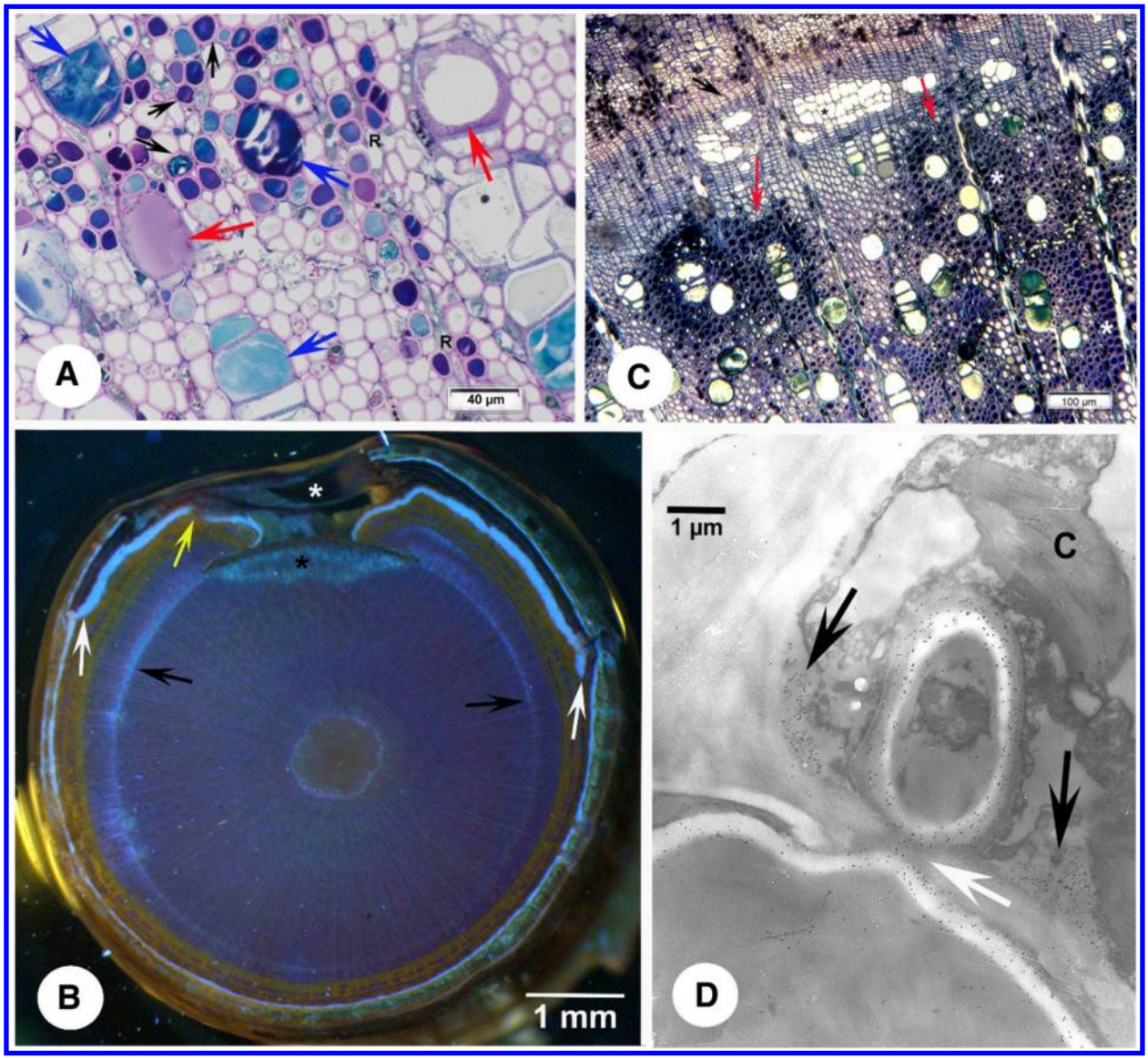

Fig. 7. A, After inoculation with *Phytophthora ramorum*, several vessels, part of a compartmentalized zone, in a stem of yellow birch are occluded by gels. Some gels are stained by toluidine blue O (blue arrows), suggesting the presence of phenols, while others in red have affinity for basic fuchsin (red arrows). Many of the parenchyma and fiber cells (black arrows) around these vessels have also accumulated phenolic compounds. R = Ray cells. **B,** A new periderm, revealed under UV illumination after quenching lignin autofluorescence with phloroglucinol-HCl, has formed (between white arrows) in this sugar maple stem and limits the extent of necrotic tissues in the bark (white asterisk). Discontinuities are visible in the new periderm (e.g., yellow arrow). The invaded xylem is limited (black asterisk) and surrounded by fluorescing cells that have likely accumulated phenols, like other cells (black arrows) laid down by the cambium in reaction to the inoculation. **C,** Several cells corresponding to a barrier zone (wall 4) are filled with phenols stained by toluidine blue O (red arrows). Similar cells are also components of a wall 3 zone (asterisks). Black arrow = Cambial zone. **D,** Intense immunolabeling for β-1,3-glucans suggesting the presence of callose over a papilla (black arrows) of a parenchyma cell in a balsam fir needle. The pathogen coming from a tracheid has penetrated the parenchyma cell through a pit (white arrow). The labeling is obvious over the *P. ramorum* wall. C = Chloroplast.

In the United States, studies were also carried out to assess the susceptibility of various plant species. Those of particular interest for Canada are listed in Table 1. For instance, Tooley and Kyde (2007) found that sugar maple and black walnut were among the most resistant species they have tested using stem inoculations. In Canada, a similar trend for sugar maple was also reported (Simard et al. 2010). In another study, the seedlings of some forest understory plants were spray-inoculated with sporangia. Leaf lesions were particularly noticeable on staghorn sumac (*Rhus typhina*), eastern redbud (*Cercis canadensis*), and winterberry (*Ilex verticillata*) (Tooley and Browning 2009). These plants are native to Canada and unknown as hosts of *P. ramorum*. In the latter study, black locust (*Robinia pseudoacacia*), an exotic tree abundantly planted in Canada where it is naturalized in some areas and not reported as a host, was also described as particularly susceptible.

In addition to testing the susceptibility to *P. ramorum*, it is often helpful to measure sporulation to estimate the propagation potential of the disease via diverse host species. Unlike the expression of symptoms, a Canadian study did not find that sporulation differed between wounded and unwounded leaves (Jinek et al. 2011). Sporangia production was noted on the foliage of all hardwood species following plant-dipping, but was particularly prominent on white ash and yellow birch. On conifers, needles of balsam fir supported more sporulation than those of tamarack. Although in some species, such as tamarack, sporulation seemed low at 1.8 sporangia/cm^2 of needle lesion, this was far from negligible, and this rate that seems weak at first glance may be due to low humidity of 85% used in the experiment. As already reported by others (Denman et al. 2009), sporulation was also observed on some asymptomatic leaves and needles, with the highest level of sporulation occurring on yellow birch and balsam fir. Sporulation on the foliage of different woody species that occur in Canada was evaluated by others (Table 1).

Management

As part of collaborative research projects among the CFS, CFIA, and AAFC, various treatments have been evaluated for their ability to protect susceptible plants from infection by *P. ramorum*. One challenge has been the limited space available in appropriate containment facilities for plant trials with *P. ramorum*. At the NRCan-CFS-PFC lab and the CFIA Sidney lab, in vitro tests have been used to screen chemical fungicides, disinfectants, and biocontrol agents in dual culture with *P. ramorum*. Detached leaf assays have been used to evaluate response of *P. ramorum* isolates to these control agents, and to test the compatibility of biocontrol agents with each other and with chemical fungicides (Becker et al. 2010a, b; Elliott et al. 2008, 2009a).

Chemical fungicides. In a study at the NRCan-CFS-PFC laboratory, nine isolates of *P. ramorum* were screened against systemic and contact fungicides in vitro for control of mycelial growth and zoospore germination, and in planta for suppression of lesion expansion on rhododendron foliage (Elliott et al. 2015). Three isolates from each of the clonal lineages, NA1, NA2, and EU1, were used in the in vitro tests and one isolate from each clonal lineage was used in the plant tests.

Systemic fungicides were the most effective at preventing mycelial growth and zoospore germination of *P. ramorum*, Subdue Maxx (metalaxyl 24%) being the most inhibitory. The EC_{50} for zoospore germination inhibition was much less than that for mycelial growth inhibition for most fungicides tested. Subdue Maxx had the lowest EC_{50} for both mycelial growth inhibition and zoospore germination inhibition for all isolates. There were significant differences in the amount of zoospore inhibition among the three clonal lineages for five of the fungicides. EC_{50} was higher for zoospore germination inhibition of the EU1 isolates by two strobilurin fungicides, indicating possible cross-resistance in this group.

The results from testing on foliage of host plants at the labeled rate supported the in vitro results, the reduction of lesion size being more pronounced when treated with Subdue Maxx. Development of resistance to some chemicals used for routine control of *P. ramorum* in the nursery should be monitored, especially in the EU1 and NA2 populations.

Biological control systems. *In vitro studies.* Some of the most promising fungi used in biocontrol systems are *Trichoderma* spp. (Harman et al. 2004), which are found in soil and are often abundant in composts. In ongoing studies, Canadian researchers at the NRCan-CFS-PFC lab are investigating the antagonistic and biological properties of several different *Trichoderma* spp. in terms of their efficacy against *P. ramorum* (Becker et al. 2011; Elliott et al. 2009a). Several tested *Trichoderma* spp., including *T. atroviride*, *T. koningii*, and *T. virens*, had the ability to overgrow and directly kill *P. ramorum*

Table 1. Host plant species that are endemic to Canada and have been tested for susceptibility to infection and/or production of inoculum by *Phytophthora ramorum*. Details of the behavior of each host can be found in the references.

Host	Common name	Infection	Sporulation	References
Abies balsamea	Balsam fir	Foliage, stem, roots	Foliage	Simard et al. (2010), Tsae et al. (2012)
Acer circinatum	Vine maple		Foliage	Parke et al. (2002)
Acer saccharum	Sugar maple	Stem		Tooley and Kyde (2007)
Alnus rubra	Red alder		Foliage	Parke et al. (2002)
Amelanchier laevis	Service berry		Foliage	Tooley and Browning (2009)
Arbutus menziesii	Pacific madrone	Foliage	Foliage	Elliott et al. (2011), Parke et al. (2002)
Betula alleghaniensis	Yellow birch	Foliage, stem	Foliage	Simard et al. (2010)
Cercis candensis	Eastern redbud	Foliage	Foliage	Tooley and Browning (2009)
Cornus sericea	Red-osier dogwood		Foliage	Tooley and Browning (2009)
Fraxinus americana	White ash	Foliage, stem	Foliage	Simard et al. (2010)
Gaultheria shallon	Salal	Foliage	Foliage	Elliott et al. (2011), Parke et al. (2002)
Ilex verticillata	Winterberry	Foliage		Tooley and Browning (2009)
Juglans nigra	Black walnut	Stem		Tooley and Kyde (2007)
Larix laricina	Tamarack	Foliage, stem	Foliage	Simard et al. (2010)
Mahonia nervosa	Oregon grape	Foliage		Elliott et al. (2011)
Quercus garryana	Oregon white oak		Foliage	Parke et al. (2002)
Quercus rubra	Red oak	Foliage, stem, roots	Foliage	Simard et al. (2010), Tsae et al. (2012)
Rhododendron macrophyllum	Pacific rhododendron		Foliage	Parke et al. (2002)
Rhus typhina	Staghorn sumac	Foliage	Foliage	Tooley and Browning (2009)
Robinia pseudoacacia	Black locust	Foliage	Foliage	Tooley and Browning (2009)
Rosa multiflora	Multiflora rose	Foliage		Tooley and Browning (2009)
Rubus allegheniensis	Alleghany blackberry	Foliage	Foliage	Tooley and Browning (2009)
Syringa vulgaris	Lilac	Foliage	Foliage	Tooley and Browning (2009)
Vaccinium ovatum	Evergreen huckleberry	Foliage	Foliage	Parke et al. (2002)

in dual culture. The effects of *Trichoderma* metabolites on *P. ramorum* (antibiosis) were investigated using a microplate assay. The species that produced the most inhibitory extracts were *T. polysporum*, *T. pseudokonigii*, and *T. harzianum* (99, 73, and 68% inhibition, respectively). *Trichoderma* isolates were also tested for their ability to tolerate chemical controls that are registered in Canada by measuring their growth on media containing either Aliette (fosetyl-Al 80%) or Subdue Maxx (metalaxyl 24%). All isolates were inhibited by Aliette, but many isolates were tolerant to Subdue Maxx. Thus, we could combine or alternate promising *Trichoderma* isolates with Subdue Maxx in an integrated pest management approach.

In another study, biocontrol products containing *Bacillus subtilis* strain QST 713 were very effective in inhibiting of *P. ramorum* in vitro. When compatibility of bacterial products with material containing *Trichoderma* was tested, *B. subtilis* was inhibitory to *Trichoderma*, but the product Actinovate (*Streptomyces lydicus*) was compatible and did not appear to limit growth of the fungal biocontrol agent, implying that these products have the potential to be used in combination (Elliott et al. 2009a).

Whole plant studies. In a study of preventive treatments applied to foliage, biocontrol and chemical fungicides were applied to plants in the greenhouse, then leaves were excised and infected with *P. ramorum* and the response to infection evaluated in the lab (Becker et al. 2010b). Treatments with Rhapsody (*Bacillus* sp.) and Actinovate (*Streptomyces lydicus*) biocontrol products to plants tended to reduce the number of leaves infected by *P. ramorum* when compared with controls, although these results were not significantly different.

Candidate treatments have been further tested in whole-plant containment trials performed in AAFC's containment facilities (Bailey et al. 2012). Several of the biocontrol products suppressed the development of *P. ramorum* compared with the non-treated control plants. The commercial product Actinovate reduced the severity of symptoms by about 50% and improved plant growth, but the effectiveness of all tested products was considered to be lower than acceptable for a commercial nursery (Bailey et al. 2012). This included the Aliette (fosetyl-Al) fungicide, which was the only fungicide that was registered in Canada for control of *P. ramorum* at the time of the study.

In spite of promising results with biocontrol agents described above, management of *P. ramorum* using these products on susceptible hosts will be difficult to achieve. The level of disease reduction in these studies was not acceptable for commercial use. Pathogen susceptibility to biocontrol agents was dependent on the isolate and lineage. Therefore, we suggest that management of *P. ramorum* must rely first on prevention through sanitation and disinfestation, and then inoculum reduction can be envisaged using biocontrol agents.

Disinfectants. Both fungicides and disinfectants play a role in the containment and eradication of *P. ramorum* in nurseries. All fungicides tested so far do not kill *P. ramorum* in established lesions on plants, but do provide prevention of symptom development on the host. Disinfectants are aimed at controlling the spread of the pathogen in the environment usually by preventing outward growth or by killing reproductive propagules.

Several chemical disinfectants used in various stages of nursery production were tested by the NRCan-CFS-PFC lab and the CFIA Sidney lab for their ability to inhibit mycelial growth, reduce the number of colony forming units (cfu), and prevent germination of sporangia of *P. ramorum*.

The disinfectants Chemprocide 1.35% (didecyl dimethyl ammonium chloride 7.5%, isopropyl alcohol 10%, ethanol 1.5%) and Javex bleach (sodium hypochlorite 3 to 7%) at 15% provided complete sanitization on all plastic and metal surfaces when given 1, 30, or 60 min exposure time. A 5% concentration of Javex bleach was just as effective as the higher concentration at 30 and 60 min exposure, but 1 min exposure was only effective 80% of the time. Bleach is both an inexpensive and highly effective disinfectant that may be used to prevent the spread of *P. ramorum* in greenhouse and nursery situations (James et al. 2012), but is not recommended for use on metal surfaces due to its corrosive nature.

Biological control of stump sprouting. Resprouting stumps can be a reservoir of *P. ramorum* inoculum (Fig. 8A). In areas where the application of herbicides is not permitted, a biocontrol treatment would be an indispensable alternative. A technique developed by researchers at the NRCan-CFS-PFC lab for treatment of stumps with the sap-rotting fungus *Chondrostereum purpureum* (Pers.) Pouzar has been shown to be effective for suppressing resprouting on several species, most notably red alder (Becker et al. 2005). A study of the ability of *C. purpureum* to suppress resprouting was conducted on stumps of two major host species, tanoak and California bay laurel. The tanoak field trial was established in 2009 near Brookings, Oregon, and a trial on bay laurel near Soquel, California, in spring 2013. Results of field testing showed that *C. purpureum* was able to colonize the stumps of tanoak following treatment, and was also found occurring naturally on tanoak logs and stumps (Fig. 8B).

Laboratory testing of three California isolates of *C. purpureum* indicated that the fungus can colonize bay laurel stems, although it has not been reported on this host. The Chontrol bioherbicide (active ingredient: *C. purpureum*) developed by Canadian researchers at the PFC was tested on California bay laurel. When the percent of the total circumference containing live resprouts was considered, Chontrol had less resprouting than the formulation without *C. purpureum* and untreated stumps, but more than the Garlon 4 (Triclopyr 60.45%) (M. Elliott, unpublished data). Formulations of *C. purpureum* appear to have some effect on reducing resprouting in tanoak and bay laurel, but herbicide treatments were the most effective and rapid. Over time, applications of *C. purpureum* may be a more permanent solution as the stumps begin to decay.

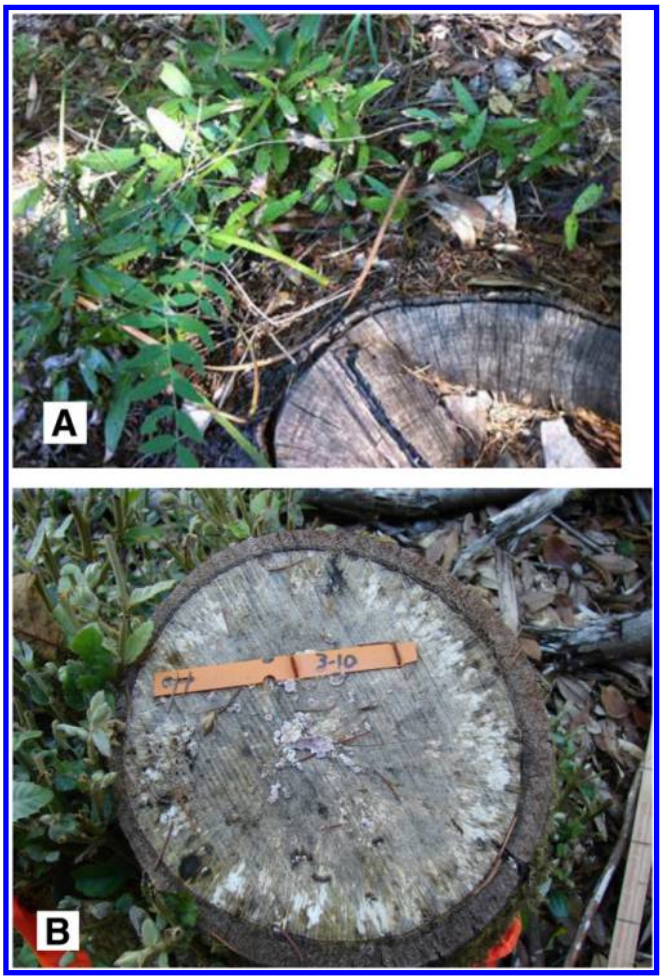

Fig. 8. A, California bay laurel (*Umbellularia californica*) stump with resprouts that are symptomatic for *Phytophthora ramorum*. **B,** The biocontrol fungus *Chondrostereum purpureum* fruiting on a tanoak (*Notholithocarpus densiflorus*) stump.

Research Gaps and Future Challenges

Research priorities and relevant documents are important tools that allow scientists, research organizations, and policy makers

(e.g., CFS, CFIA, and APHIS) to assess the state of knowledge and identify the highest priority areas for future research. The Canadian *P. ramorum* and emerging *Phytophthora* forest diseases research program appears to follow a pattern of evolution shown with other invasive alien species where early studies focus mainly on basic biology and progresses toward more management-oriented questions. These questions revolve around the research previously described on risk analysis, pathogen detection and diagnostics, host symptoms, sporulation and resistance, eradication, remediation and regulatory issues, and finally best management practices. Periodic reassessment of research needs is recommended as new findings and new problems arise. The following areas of potential research interest and needs are provided.

Risk assessment. Ongoing revision of the existing CFIA PRA documents (the last full PRA was published in 2009) should include the latest research findings and information on *P. ramorum* in North America and Europe to meet the National Forest Pest Strategy (NFPS) requirements. This would include risk assessment of the new EU2 lineage of *P. ramorum* and its potential threat to the Canadian nursery industry and forest ecosystems. Stream monitoring surveys for *P. ramorum* and other *Phytophthora* spp. in selected eastern and western Canadian urban and forested sites are needed to determine potential threats to our forests. These will also provide information on the effectiveness of nursery best management practices and eradication measures. Determining the epidemiological significance of the presence of *Phytophthora* spp. in streams is also essential. In addition, investigating the impact of other established invasive alien *Phytophthora* spp. in Canada (e.g., *P. lateralis* and *P. cinnamomi*) on Canadian flora is crucial. Further development of genomics-enhanced forest disease (e.g., *P. ramorum*) diagnostics and monitoring is needed. The overall goal is to overcome hurdles to early detection of invasive pathogens such as *P. ramorum* by translating genomic resources into integrated genomics-based tools to help detect and monitor new and emerging pathogens. This would immensely improve phytosanitary measures and regulatory processes. Finally, a clearer understanding of the climatic factors that constrain *P. ramorum* distribution would help to better identify areas at risk of invasion, which currently vary widely depending on the modeling approach employed.

An examination of relative economic impacts would clarify the potential losses to the Canadian horticulture industry from increased phytosanitary regulation, as well as the impact to Canadian forest industries and forest product exports should *P. ramorum* become established in Canadian wildlands. Development of forest pest diagnostic and monitoring capacity is strongly supported by regulatory agencies such as CFIA and USDA-APHIS and addresses key issues of the Canadian Forest Invasive Alien Species and the NFPS initiatives.

Biology. Further assessment of Canadian plant species, including conifer and broadleaf trees, is necessary to determine their susceptibility and whether there are potential Canadian sporulating hosts such as California bay laurel or Japanese larch. An investigation of survival of *P. ramorum* in soils, roots, leaves, larch needles, tree stem tissue, and selected understory forest vegetation under Canadian winter conditions is needed. To facilitate detection of *P. ramorum* in asymptomatic, chemically treated plants imported to Canada, we require more knowledge about the factors involved in the breaking of chlamydospore dormancy and pathogen latency after chemical treatment. Further determination of pathogenesis and resistance mechanisms to infection by *P. ramorum* in selected Canadian conifer and broadleaf tree species using histopathological approaches is also essential. For all of these biological studies, the differences in the behavior of the fourth known clonal lineage, EU2, should be examined.

Management. To ensure continued export of Canadian wood products, a thorough evaluation of the efficacy of heat treatment on *P. ramorum* as related to current lumber treatment standards is needed. This would be facilitated by research that clarifies the extent of colonization and length of survival of *P. ramorum* in untreated conifer and broadleaf wood and wood products sourced from infected trees. Other areas of research that are needed include further screening of current biocontrol products and naturally occurring fungal and bacterial antagonists as potential control agents of *P. ramorum*, such as exploring organisms found in *Phytophthora*-suppressive bark mulch substrates. In addition, it is very important to find chemicals that kill the pathogen in the host and to examine resistance and cross-resistance to fungicides among the clonal lineages of *P. ramorum.*

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Simon Francis Shamoun


Danny Rioux


Brenda Callan


Delano James


Richard C. Hamelin


Guillaume J. Bilodeau


Marianne Elliott


C. Andre Lévesque


Elisa Becker


Dan McKenney


John Pedlar


Karen Bailey


Stephan C. Brière


Kurt Niquidet


Eric Allen

Dr. Simon Francis Shamoun is a research scientist with Natural Resources Canada, Canadian Forest Service at the Pacific Forestry Centre in Victoria, British Columbia. He graduated with B.Sc. honors in forest sciences (1972) from the University of Mosul, Nineveh, Mesopotamia (Iraq); M.Sc. in plant pathology (1979) from North Carolina State University; and Ph.D. in plant pathology (1988) from the University of Arkansas, U.S.A. His current research studies include biology, molecular diagnostic, and development of mitigation tools for management of *Phytophthora ramorum*. Furthermore, he is investigating the impact of wood decay fungi (e.g., *Heterobasidion* spp.) and other indigenous and emerging invasive alien forest pathogens associated with wood products intended for international trade, with an objective to protecting both Canadian forest ecosystems and market access for Canadian wood products. In addition, Dr. Shamoun is continuing his research on biological control of native and invasive alien forest pathogens, including the potential use of dsRNA genetic elements "mycoviruses" in the *Heterobasidion* species complex. He is an adjunct professor at Thompson Rivers University, Department of Biological Sciences; associate editor for botany; PLOS ONE; Archives of Phytopathology and Plant Protection; and Tropical Plant Pathology. He is a deputy coordinator of the IUFRO working unit 7.02.11.

Danny Rioux is a research scientist working at the Laurentian Forestry Center in Quebec City (Natural Resources Canada - Canadian Forest Service). He is an adjunct professor at Université Laval in the Department of Forest and Wood Sciences. He received his bachelor's degree in forest engineering from Université Laval in 1983 and he completed his Ph.D. at the same university in 1989. He was president of the Quebec Society for the Protection of Plants in 2004, editor-in-chief of the *Phytoprotection* journal (2005-2008), and he is currently a senior editor for *Plant Disease*. Most of his studies aim to understand host-pathogen interactions in microscopy with tree diseases such as scleroderris canker, Dutch elm disease, and sudden oak death. Lately, his efforts have been mainly devoted to evaluate the susceptibility of tree species common in eastern Canada to sudden oak death and to recover and protect butternut affected by a canker that threatens its survival.

Brenda Callan is a research scientist with Natural Resources Canada, Canadian Forest Service at the Pacific Forestry Centre in Victoria, British Columbia. She was trained as a plant pathologist at Washington State University (M.Sc. and Ph.D.). Her publications include diagnostic manuals and new tree and plant disease records for BC and Canada. She currently conducts research on the detection and identification of fungi associated with commodities such as conifer lumber and logs.

Delano James is a research scientist at the Sidney Laboratory – Centre for Plant Health of the Canadian Food Inspection Agency. He is also an adjunct professor in the Department of Biology, University of Victoria, BC. He received his Ph.D. in agriculture from the University of the West Indies. His primary areas of research focus on molecular characterization of pests of quarantine and economic significance, and the development of nucleic acid and serology-based tools for rapid and accurate detection of these disease causing agents. He conducts research on the analysis, detection, molecular characterization, and control of viruses, including viruses that infect fungi. Other areas of research include identification and development of chemicals and strategies for chemotherapy, and identification of causal agents of important uncharacterized diseases. His various research activities provide essential support to the virus testing capabilities of CFIA in its mandate of disease control and prevention.

Dr. Richard Hamelin is a professor at the University of British Columbia and Université Laval. Dr. Hamelin obtained a B.Sc. from McGill University in 1982, a master's degree in pest management from Simon Fraser University in 1986, and a Ph.D. from the University of Kentucky in 1990. He has 30 years of experience in forest health research and has published over 120 peer-reviewed scientific papers. His work aims at using genomics to better understand forest disease epidemics and to design detection and monitoring methods to prevent invasions of pests and pathogens that threaten forests. He was president

of the Canadian Phytopathological Society and the Quebec Society for Plant Protection and was awarded the International Unions of Forest Research Organization Scientific Achievement Award (2014), the Queen Elizabeth II Diamond Jubilee award (2012), and merit awards from Natural Resources Canada (2008), the Canadian Forest Service (2008), the Canadian Food Inspection Agency (2007), and the Quebec Society for Plant Protection (2008) for his pioneering work on the application of genomics in forest protection.

Dr. Guillaume Bilodeau received his Ph.D. in 2008 from Laval University (Quebec, Canada) in the department of microbiology with Dr. Richard Hamelin at the Laurentian Forestry Centre, Quebec, Canada, with thesis subject entitled, "Detection and genomics of *Phytophthora ramorum*, causal agent of sudden oak death." In 2008, Dr. Bilodeau moved to Salinas, California, for postdoctoral research in the laboratory of Dr. Frank Martin, USDA-ARS, where he worked on the development of a molecular detection and quantification tool for plant pathogenic fungi (*Phytophthora* and *Verticillium*) using DNA detection methods. In 2011, he joined the Canadian Food Inspection Agency (CFIA), Ottawa Plant Laboratory (Fallowfield), as research scientist in the Plant Pathogens Identification Research Lab (PIRL) where he plans, organizes, coordinates, and conducts research and development of technologies for detection and identification of plant pests (fungi-oomycetes) of regulatory significance in seed, agriculture, and forestry. Dr. Bilodeau is also collaborating in multiple genomic projects and his expertise is in fungal/oomycete detection and genotyping real-time PCR, nucleic acid extraction, and molecular biology using genomics. He developed multiple detection and identification tools for helping diagnostic labs. He is also associated professor at Laval University, Quebec City, in the Department of Biochemistry, Microbiology, and Bioinformatics.

Marianne Elliott is a plant pathologist at Washington State University, Puyallup Research and Extension Center. She completed a Ph.D. in forest resources at the University of Washington in 2005 and did post-doctoral studies on biology and management of *Phytophthora ramorum* at the Canadian Forestry Centre, Pacific Forestry Centre in Victoria, British Columbia. Her current research is on management of *Phytophthora* diseases and stream surveys for *Phytophthora* species.

André Lévesque is a research scientist with the biodiversity group of Agriculture and Agri-Food Canada, Ottawa, and is the study co-leader for the mycology/microbiology unit. He is adjunct professor in the Biology Department of Carleton University, Ottawa. He graduated with a B.Sc. in agriculture from McGill University, Montréal, a master's degree in pest management (1985), and a Ph.D. (1990) in plant pathology from Simon Fraser University, Burnaby, British Columbia. He was president of the Canadian Phytopathological Society in 2005-2006. His current research is on molecular taxonomy, phylogenomics, and molecular ecology of fungi, specializing in zoosporic fungi and oomycetes.

Dr. Elisa Becker is a research scientist at the Canadian Forest Service working at the Pacific Forestry Centre in Victoria, British Columbia. Her background is in molecular biology and genetics with a focus on fungi and oomycetes, including those that cause diseases of forest trees as well as fungi that may be used as biological control agents. Her research on soil fungi that are antagonistic to the SOD pathogen *Phytophthora ramorum* has identified candidate species that may be used to limit the spread of this invasive pathogen from infected nursery plants to native forests. Her present interests include the pathogenesis and wood decay of living trees, and climate change impacts on forest disease, with an emphasis on the effects of drought. Dr. Becker's current projects include collaborative studies of both Douglas-fir and western red cedar trees with goals of selecting elite tree families for resistance and tolerance to multiple stressors, including drought and root diseases.

Dan McKenney is a senior scientist and team leader with the Canadian Forest Service in Sault Ste. Marie. He is also currently an adjunct professor at the University of Guelph, McMaster, and the University of Toronto. His research interests include the development and integration of climate data in economic and ecological studies. He has a Ph.D. in forest economics and policy from the Australian National University, a master's in resource economics from the University of Guelph, and a B.Sc. in forest science from Texas A&M University.

John Pedlar has an M.Sc. in landscape ecology from the University of Carleton. He works as a biologist for the Canadian Forest Service (CFS) at the Great Lakes Forestry Centre in Sault Ste. Marie, Ontario. His work focuses on economic and ecological issues related to invasive forest insects and climate change. Recently he has served as a member on two CFS task groups, exploring the topics of assisted migration and climate change impacts on timber supply in Canada.

Karen Bailey is a research scientist with Agriculture and Agri-Food Canada in Saskatoon, Saskatchewan. She was trained as a plant pathologist at the University of Guelph (B.Sc. agriculture, M.Sc.) and the University of Saskatchewan (Ph.D.). Her research has focused on integrated pest management studying the impact of breeding and agronomics on soilborne diseases of field crops and the development of novel pest control products using fungi for the management of weeds in horticulture, agriculture, and agro-forestry. She has received the Canadian Phytopathological Society Award for Plant Disease Management, CPS Award for Outstanding Research, and the Queen's Diamond Jubilee Medal for her scientific contributions to agriculture in Canada.

Mr. Stephan C. Brière is a plant pathologist and the manager of the Plant Pathology Laboratory at the Ottawa Plant Laboratory of the Canadian Food Inspection Agency in Ottawa, ON, Canada. He has over 25 years of training and experience in the plant protection field working as a mycologist and plant pathologist. His diverse knowledge covers biology, epidemiology, and disease diagnosis of fungi, bacteria, and viruses. Mr. Brière has worked in a variety of organizational categories ranging from plant disease diagnostics, plant pathogen containment, research, biocontrol, teaching, industry, and government. His work contributes greatly to Canada's National Plant Protection programs, setting a standard to prevent the introduction and spread of invasive species to Canada's agriculture and forestry industry. In his current role, he works directly in support of Canada's national plant protection programs, standards, policies, regulations, and initiatives to prevent the introduction and spread of invasive plant pathogens that threaten Canada's crops and forests. He has been responsible for all *Phytophthora ramorum* regulatory import and survey diagnostic testing for Canada since 2002.

Kurt Niquidet is the manager of the Forest Industry, Trade and Economics Research Group at the Pacific Forestry Centre in Victoria, British Columbia. Kurt conducts research on forest sector competitiveness, bioenergy, and the economics of forest disturbances. Before joining the Canadian Forest Service in 2009, he spent time in New Zealand as a lecturer in forest economics and did a post-doc at the University of Victoria. He has a doctorate in economic geography from the University of Groningen, masters in economics from the University of Victoria, and a forestry degree from the University of British Columbia.

Eric Allen is head of the Forest Invasive Alien Team with the Canadian Forest Service at the Pacific Forestry Centre in Victoria, Canada. For the past 20 years, he has worked extensively on non-indigenous species that impact forest ecosystems; their biologies, their movement with international trade, and the assessment of mitigation measures. He is the chair of the International Forestry Quarantine Research Group, and the North American Plant Protection Organization (NAPPO) expert group on forestry systems approaches, and is a member of the International Plant Protection Convention (IPPC) Technical Panel on Forest Quarantine.

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