Phytophthora ramorum: Update on the Impact and Wider Consequences of the Epidemic in Britain[1]

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Abstract

Many new *Phytophthora* pathogens have arrived in the UK via the plant trade in recent decades, but arguably *Phytophthora ramorum* has been one of the most significant introductions to affect trees. From 2002 onwards during the early stages of the epidemic, the first impacts of *P. ramorum* were seen in ornamental plant nurseries, then affecting valuable heritage plants in gardens important to the tourist trade, and eventually in broadleaf dominated woodlands (Brasier and others 2004). In the latter, a few tree species, such as European beech (*Fagus sylvatica*) and sweet chestnut (*Castanea sativa*), were occasionally affected, although native European oaks proved to be of low susceptibility in contrast to native North American oak species. However, rhododendron, in the form of valued ornamental cultivars in gardens or the invasive non-native shrub *Rhododendron ponticum*, was the common host across all environments. It also proved essential to the epidemic because it sustained pathogen sporulation, whereas the bole cankered tree hosts did not. As a harmful organism listed within the European Union EC Plant Health Directive (2000/29/EC), phytosanitary measures required eradication or disease containment achieved through the removal of sporulating hosts. Therefore, control measures against *P. ramorum* focused on rhododendron removal, and the range of tree bole hosts affected fit with the American 'model,' with the worst affected species in the *Fagaceae* family.

However, in 2009 an unexpected change occurred in the disease dynamic in Britain. Across southwest England, there were several findings of *P. ramorum*-infected plantation-grown Japanese larch (*Larix kaempferi*), but they were not close to infected rhododendron (Webber and others 2010). Widespread mortality was also observed as larch stems were girdled and the infected phloem tissue underwent a series of chemical changes incited by *P. ramorum* colonization. Not only Japanese larch but also European (*L. decidua*) and hybrid larch (*L.* x *eurolepis*) were also found affected by the ramorum-induced dieback. Moreover, *P. ramorum* was found to sporulate profusely on infected larch needles, particularly those of Japanese larch, with the numbers of spores far exceeding those produced from rhododendron foliage and California bay laurel (Harris and Webber 2016).

As larch was the third most commonly grown conifer species (after spruce and pine) and *P. ramorum* was sporadically established throughout western Britain on rhododendron, the host jump from rhododendron allowed the epidemic to develop on larch almost simultaneously across climatically suitable areas on a landscape scale. Thousands of hectares of near contiguous larch plantations were affected in some regions, and regular aerial surveillance by helicopter was put in place from 2010 onwards as part of the measures to detect and contain the spread. Between 2009 and 2016, almost 20,000 hectares (~50,000 acres) of larch throughout the UK were affected by the disease, with millions of trees felled to contain disease outbreaks. Large management zones have been set up in southern Wales and southwest Scotland (Forestry Commission 2014), and satellite outbreaks are managed on a site by site basis. The most conducive climate for disease development is in the western British Isles, due to mild winters and high

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rainfall. Years with above average rainfall, such as in 2012, can result in striking increases in disease development associated with an upsurge in larch mortality the following year.

As a sporulating host, removal of infected larch is critical to managing the epidemic, slowing disease spread, and allowing remaining larch stocks to stay healthy for as long as possible so they can be harvested without a "biosecurity penalty." The latter alludes to the loss of valuable bark bi-products through infection as well as the need to use a network of inspected sawmills licensed to process the lumber from infected larch stands. Where felling is not an option, the use of herbicide injection is also being explored with the aim of achieving a rapid kill of infected trees, reducing the potential of infected foliage to release spores into the environment. If the disease is not controlled in infected larch stands, neighboring plants and trees also frequently become infected. For example, other conifer species including Douglas-fir (*Pseudotsuga menziesii*), grand fir (*Abies grandis*), noble fir (*A. procera*), and western hemlock (*Tsuga heterophylla*) can suffer significant stem and branch infections and show symptoms of crown dieback, although only when growing in close proximity to infected larch.

A further, and more recent complication in the invasion of *P. ramorum* across the UK, is the discovery of the novel EU2 lineage (Van Poucke and others 2012) in addition to the widespread EU1 lineage. So far, the EU2 has only been found in the UK where it is limited to Northern Ireland and southwest Scotland (King and others 2015). Its distribution is, however, expanding, and in parts of southwest Scotland, the distributions of the EU1 and EU2 are now close to overlapping (fig. 1). The intensive sampling of larch across Britain to test for the presence of both EU1 and EU2 lineages of *P. ramorum* has also provided surprising insights into how frequently other Phytophthoras are associated with larch and other conifer species, such as *P. pseudosyringae* and *P. gonapodyides*. Like *P. ramorum*, both of these *Phytophthora* species produce aerial cankers on branches of mature larch trees. This raises the possibility that they may also infect and sporulate on larch needles as *P. ramorum* does, thereby providing the inoculum for aerial bark infections.

The continuing epidemic has provided a graphic example of the highly unpredictable outcome of a pathogen introduction and heighted public awareness of the environmental and economic costs that can result from such events. The changing nature of the epidemic is further emphasized by recent observations made in some remnant ancient semi-natural woodlands which suggest that ramorum disease may now be cycling on sweet chestnut, in the absence of larch or rhododendron. Sweet chestnut can apparently act as both bole host and sporulating host, although levels of sporulation by *P. ramorum* on sweet chestnut leaves are lower than those on larch needles (Harris and Webber 2016). Current management strategies concentrate on the clearance of infected larch, but if infected sweet chestnut can provide alternative disease foci, their management needs to be reconsidered in light of their sporulation potential.

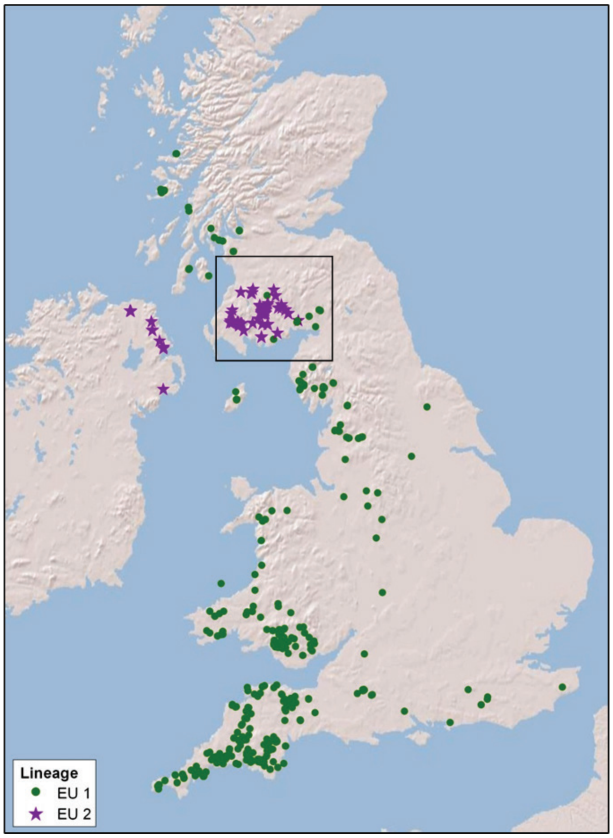

Figure 1—Map showing the distribution of EU1 (green dots) and EU2 (purple stars) lineages of *P. ramorum* infecting larch in the UK at the end of 2015.

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