PHYTOPHTHORA RAMORUM IN LARCH: FROM EPIDEMIOLOGY TO HOST RESISTANCE

Title presented at workshop:

UNDERSTANDING SUDDEN LARCH DEATH—FROM EPIDEMIOLOGY TO HOST RESISTANCE

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Phytophthora ramorum is a forest pathogen known for two major epidemics, sudden oak death in the USA, which began in the 1990s (Rizzo et al. 2002) and, more recently, sudden larch death in the United Kingdom in which *P. ramorum* was first found infecting Japanese larch in south-west England in 2009. This was the first record of *P. ramorum* infecting a conifer species in a natural situation (Webber et al. 2010). In spring 2013 there was an observed dramatic increase in the spread and severity of *P. ramorum* in larch stands across western Britain, including in the Galloway Forest. The Galloway Forest is the largest forest in the UK and provides a particularly interesting field site for studying the epidemiology of *P. ramorum* in larch as disease control legislation for the 2013 epidemic resulted in a management zone where infected stands could be retained for research rather than being immediately felled. The Galloway Forest outbreak was caused by the EU2 lineage of *P. ramorum* which is particularly virulent on Japanese larch (*Larix kaempferi*) and European larch (*Larix decidua*) (King et al. 2014), two important timber species in the UK accounting for 10 percent of all UK conifer plantations.

A better understanding of the epidemiology of sudden larch death is needed to inform management decisions and maintain larches as commercial timber species. Survivor trees within high mortality stands in the Galloway Forest suggest the possibility of natural resistance within the Japanese larch population. Understanding how the pathogen spreads within and between individuals will help to predict if survivor trees have escaped infection by chance or may actually be resistant.

In order to understand disease spread, 21 individual larch trees in each of 21 plots located in larch stands of varying ages were surveyed for disease symptoms each May and September from 2016 to 2018. In addition to recording symptoms on needles, shoots, branches, and main stem, samples of lesion material were taken from central trees in each plot for pathogen isolation by selective media and qPCR to confirm infection by *P. ramorum*. In September 2017 and 2018 symptomatic foliage was collected and 20 needles were stained with lactophenol blue and the abaxial and adaxial surfaces examined for *P. ramorum* sporulation.

Climate records from the Met Office Hadley Centre Observations provide a homogeneity-adjusted series of averaged precipitation across areas of the UK. Our study sites lie within the South Scotland area, which uses records from eight weather stations. Three of these stations are located within 50 km of our study sites.

Between the 2013 epidemic and the start of our surveys in September 2016 disease levels had been stable and spread both within and between stands was limited. Observations in our plots between 2016–2018 showed that disease spread varied between years. In the first survey in September 2016 all disease symptoms were recorded at low levels, with on average < 5 percent of each tree being affected. The main stem mortality was on average higher at 8 percent as this included the trees that had died and were recorded as 100 percent mortality (fig. 1).

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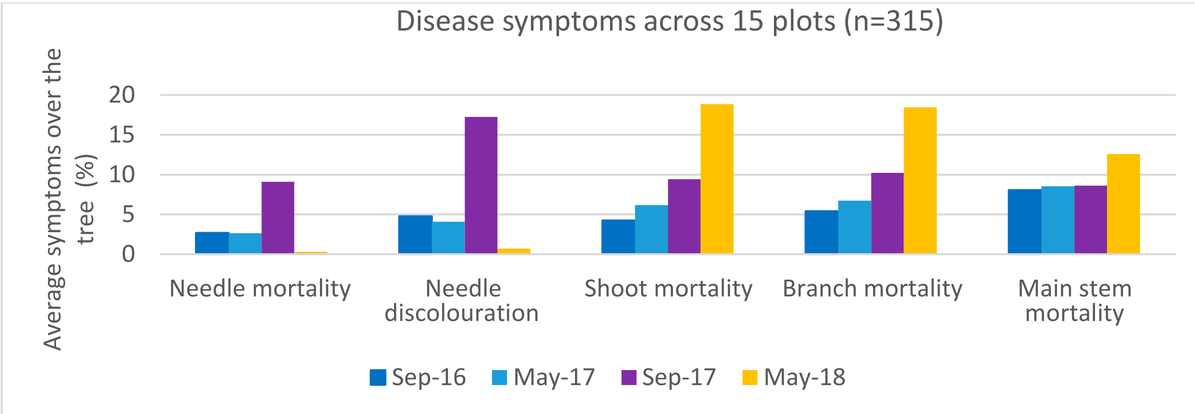

Figure 1—Results of field surveys of *P. ramorum* disease symptoms in Japanese larch in the Galloway Forest. (n = 315) between September 2016 and May 2018. Main stem mortality is a measure of mortality of the main trunk from the apex of the tree down.

Needle mortality and discolouration were similar between September 2016 and May 2017 but fine shoot and branch mortality increased slightly. Needle discolouration was notably higher in September 2017 compared with the previous September, this was followed by a doubling in the average shoot and branch mortality in May 2018 and we infer that this discoloration may have been caused by needle infection by *P. ramorum*. The adaxial and abaxial sides of sample sets of 40 needles from 5 plots were examined for sporangia production but no sporangia were observed on the needles at that assessment time. Successful isolations from lesion material have been made from trees in each plot thus confirming that *P. ramorum* is present across all the plots.

The May 2018 survey found a large increase in *P. ramorum* infection within and between stands (which was also apparent in larch across the wider region) with many trees showing symptoms for the first time in this study and stands that were previously uninfected becoming infected.

The most obvious symptom across a range of plots was a frequently occurring dieback of the fine shoots; these shoots had not flushed at all since spring and were prominent across the crown (fig. 2). These aerial infections appeared to have largely started in the fine, outer shoots of the upper crown and extended down branches towards the main stem. Suggesting significant aerial spread of infection, possibly through windborne inoculum.

There were similarities in disease expansion in the outbreaks in 2013 and 2018 but subsequent lulls in infection in the intervening years. The increase in infection seen in May 2018 brought up the question of why disease spread was much slower between the May 2013 epidemic and May 2018. Comparing our survey results over time with climate records also allows us to consider the possible links of climatic conditions to epidemic spread of *P. ramorum*.

Figure 2—Fine shoot and branch dieback on Japanese larch in Galloway Forest in May 2018. (Courtesy photo by Heather Dun)

Comparison to climate records suggests that the disease expansions observed in 2013 and 2018 were preceded by record wet summers (fig. 3). Monthly rainfall between 2012 and 2018 is highly variable compared to the 18-year average rainfall between 2000 and 2018.

Of particular interest is June rainfall in 2012 and 2017, with double average precipitation preceding both the 2013 and 2018 epidemics whereas the intervening years, in which disease expansion was much slower, had lower than average June rainfall. Less obvious but also worth noting is the higher than average rainfall in July, August, and September in both 2012 and 2017.

We observed an increase in infection of larch characterized by shoot mortality in our field sites in the spring of 2018 and this was also observed across the wider region (Forestry Commission Scotland 2018). Our observations of infection spread over the scale of individual trees allowed us to develop a more detailed understanding of how disease progresses. Previous reports of infection in larch focused on main stem lesions that caused girdling leading to whole tree mortality together with sporangia production on needles (Webber et al. 2010). Shoot dieback after infection with *P. ramorum* has been recorded in multiple woody species, including both deciduous and evergreens in the USA (Hansen et al. 2005). Our observations indicate that fine shoot infection is a mechanism of rapid disease progression in *P. ramorum* in larch.

We propose that high summer rainfall might influence the levels of infection observed at flushing in the following season. It is possible that high summer humidity would facilitate the prolific needle sporulation needed for subsequent epidemic spread. The positive relationship between infection and humidity has been well documented in *P. infestans* (Harrison and Lowe 1989) (Hirst and Stedman 1960). In sudden oak death in the USA sporangia in soil remained infectious over summer for 3 months after a rain event (Fichtner et al. 2007). It is possible that summer rainfall induces sporangia production on needles which then infect shoots over winter, becoming obvious with lack of spring flush. Alternatively the sporangia, if able to overwinter, might infect fine shoots directly in spring.

This study proposes that disease spread involves fine shoot infections and the influence of rainfall in the preceding season. Inoculation experiments would be a useful approach to further test this infection pathway of *P. ramorum* in larch and investigate the effects of climate on epidemiology.

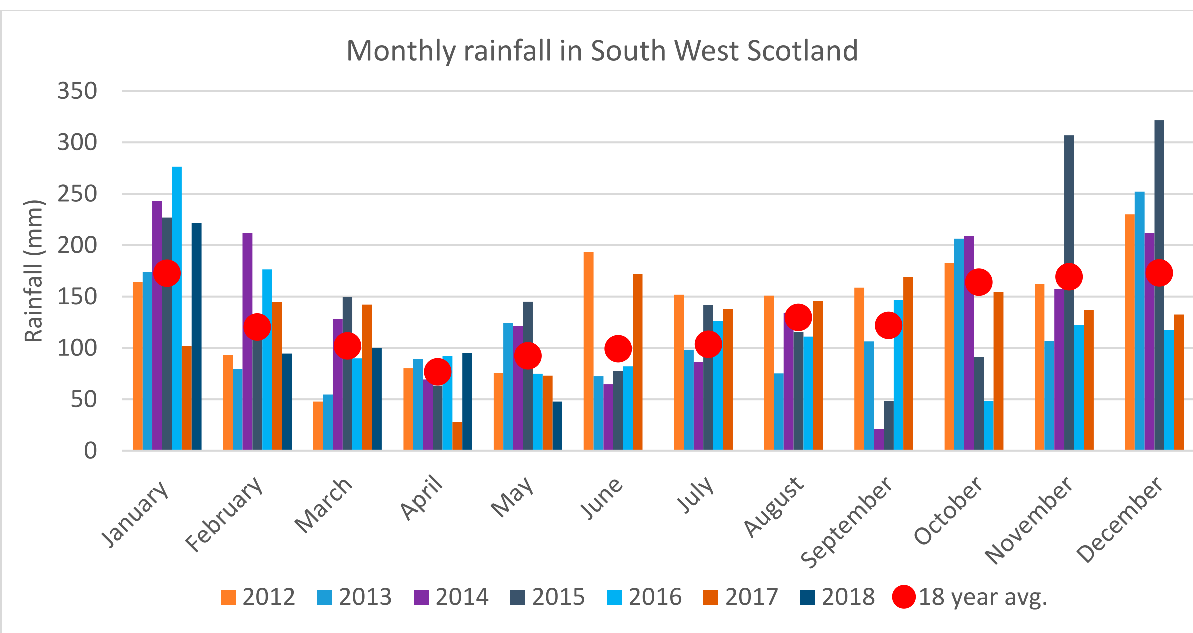

Figure 3—Monthly precipitation in south-west Scotland between 2012–2018 and 18-year average precipitation for each month.

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