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Phytophthora ramorum is a generalist plant pathogen with differences in virulence between isolates from infectious and dead-end hosts

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Summary

Variation in virulence was examined among isolates of *Phytophthora ramorum* from epidemiologically important or infectious (non-oak) and transmissive dead-end (oak) hosts from North America. Twelve isolates representative of the genetic, geographic and host range of *P. ramorum* in the western United States were inoculated on leaves of *Umbellularia californica* (bay laurel or bay) and stems of *Quercus agrifolia* (coast live oak). In spite of extreme genetic similarity among the isolates employed, and even within the same genotype, significant differences in lesion size were measured, suggesting virulence in this pathogen is also controlled by epigenetic factors. A strong positive correlation between lesion size on bay laurel and coast live oak provides experimental evidence *P. ramorum* is a generalist pathogen that lacks host specificity. Isolates from non-transmissive oaks were significantly less pathogenic both on oaks and bays than isolates from infectious hosts. These results are essential to further our understanding of the epidemiology and evolutionary potential of this pathogen. A quantitative differential in virulence of isolates from hosts with different epidemiological roles has been described for many animal diseases, but is a novel report for a plant disease.

1 Introduction

Phytophthora ramorum is a newly described plant pathogen that causes a forest disease known as sudden oak death (SOD) (Rizzo et al. 2002). This organism is unique among *Phytophthora* species of temperate forest ecosystems because of the significant aerial component of its life cycle (Davidson et al. 2005, 2008). The known distribution of the pathogen includes nurseries of ornamental plants in Europe and North America, as well as in wild woodlands of the western United States (Werres et al. 2001; Rizzo et al. 2002; Davidson et al. 2003). Recently, isolated outbreaks have also been reported in forest settings in Europe, including a significant infestation of planted larch in the UK (Brasier et al. 2004; Brasier and Webber 2010). Based on its limited geographic distribution in the wild, the severity of symptoms it can cause on some hosts and the limited genetic diversity of its populations, *P. ramorum* is regarded as an exotic pathogen of unknown origin to both Europe and the United States (Rizzo and Garbelotto 2003; Ivors et al. 2004, 2006). It has been recently shown that the infestation in the wild is linked to multiple escapes of the pathogen from nursery plants and that the pathogen is reproducing only asexually in California (Ivors et al. 2006; Mascheretti et al. 2008, 2009). Genetic evidence has further indicated the pathogen has been transferred among commercial nurseries both within North America and between North America and Europe (Goss et al. 2011). Several countries, including the United States, have imposed strict quarantines and regulations aimed at preventing the further spread of this microbe through infected ornamental plants (Anonymous 2006, 2008). Regulatory action of this scope and intensity is historically unprecedented for a generalist plant pathogen.

In nursery settings, *P. ramorum* infects many different plant species (Werres et al. 2001; Rizzo et al. 2002; Davidson et al. 2003). Symptoms include foliar necrosis, branch die-back, and, at times, lethal stem infection. The most common nursery hosts include several species and varieties within the genera *Rhododendron*, *Camellia* and *Viburnum* (arrowood). The wild-land infestation of *P. ramorum* ranges from central California to southern Oregon and seriously affects populations of coastal oaks in the section Lobatae (commonly referred to as red oaks) and the related *Notholithocarpus densiflorus* (synonym *Lithocarpus densiflorus*, tanoak) (Rizzo et al. 2002; Rizzo and Garbelotto 2003). On the US west coast, oak and tanoak stem cankers are generally lethal, while the pathogen is known to cause less serious diseases on a wide range of native hosts including coniferous and broad-leaved trees, shrubs, herbaceous plants and even ferns (Davidson et al. 2003; Rizzo and Garbelotto 2003).

While it is useful to partition hosts on the basis of severity of disease symptoms, a far more meaningful grouping is that based on the role played by each host in the epidemiology of the disease. In Californian forests, sporulation (production of deciduous sporangia) by *P. ramorum* during favourable conditions is always greatest on bay laurel trees, with less abundant sporulation observed on other hosts such as tanoak twigs and redwood needles. Conversely, sporulation on oaks has not yet been observed, and consequently, it is believed that oak-to-oak infection may be insignificant and that bay laurels may effectively represent the most important reservoir of the pathogen in oak woodlands. (Davidson et al. 2005). Further evidence that supports the role of plants such as bay laurel in the epidemiology of the disease is the fact that presence of infected bay leaves is strongly correlated with girdling stem cankers on *Quercus agrifolia* (coast live oak) (Kelly and Meentemeyer 2002; Rizzo and Garbelotto 2003), and, in fact, foliar infections of bay laurel generally precede the infection of oaks (Rizzo and Garbelotto 2003). An analogous situation has been observed in nursery settings or in European wild infestations associated with plantings of ornamental plants where rhododendrons and camellias are reported as hosts of major epidemiological importance (Brasier et al. 2004).

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