The Importance of Understory Infection by *Phytophthora ramorum* as a Means of Primary Disease Establishment in Oregon Forests¹

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Abstract

Phytophthora ramorum-infested soils have been implicated as a source of primary inoculum in natural ecosystems. Implicit in this pathway is the need for infection of understory vegetation during pathogen establishment, preceding infection of bole hosts. In support of soil dispersal, studies using artificially-inoculated soils have shown that understory inoculum can infect low-lying foliage of tanoak (*Notholithocarpus densiflorus* (Hook. & Arn.) Manos, Cannon & S.H. Oh) and California bay laurel (*Umbellularia californica* (Hook. & Arn.) Nutt.) (Fichtner et al. 2009). The lack of association between sudden oak death (SOD) and roads in Oregon, however, is inconsistent with a soil-mediated, long-distance dispersal mechanism. Regardless, *P. ramorum* can be recovered from soils at sites treated as part of the SOD eradication program (Goheen et al. 2008), as well as from streams within infested watersheds during all seasons of the year (Sutton et al. 2009). It is unknown to what extent these understory inoculum sources are responsible for establishing new disease foci, posing a risk for the continued spread of *P. ramorum* in Oregon.

We took two approaches to assess if soil or stream-borne inoculum is contributing to the establishment of *P. ramorum* infection in understory vegetation: 1) a survey of infested streams to discern the extent of streamside infection, and 2) a spatial analysis to assess if understory infection occurs independently of overstory mortality. For both studies we postulated that the presence or absence of disease gradients in the understory may indicate if infection arose from understory inoculum sources or from symptomatic overstory tanoaks presumed to have canopy infection. Transects were established adjacent to streams known to harbor inoculum or around symptomatic overstory tanoaks. Along each transect, the presence of major foliar hosts was noted; symptomatic foliage was gathered and plated in selective media to discern the presence or absence of *P. ramorum* or other *Phytophthora* spp. with increasing distance away from potential inoculum sources.

Despite the abundance of understory hosts and other *Phytophthora* spp., *P. ramorum* was not recovered from foliage along streams bearing inoculum, except when associated with overstory mortality. California bay laurel was the most common host at all locations, although understory and overstory tanoak were present at all sites. *Phytophthora nemorosa* was the most common *Phytophthora* spp. recovered, and was equally abundant directly adjacent to streams as out of the splash and flood line. *Phytophthora ramorum* was isolated from only four sites. We preferentially recovered *P. ramorum* from tanoak and out of the splash and flood line. All samples positive for *P. ramorum* were directly downhill from overstory mortality. Immediately downstream from overstory mortality we failed to recover *P. ramorum* from streamside vegetation.

A strong disease gradient was detected around SOD-positive overstory tanoaks, indicating spatial dependence upon overstory sources. Understory hosts were abundant at all sites. There was a significant, negative relationship between pathogen recovery and distance from the center of each site, lending evidence that secondary inoculum originated from overstory canopies.

We found no evidence that soil or stream-borne inoculum is causing significant infection in understory vegetation, at least during the conditions of the eradication program practiced in Oregon. Despite a decade of inoculum presence in some waterways, stream-borne inoculum is not resulting in significant stream-side infection. Rather, the majority of understory infection is associated with overstory mortality. The lack of understory infection independent of these overstory sources implies that the movement of soil-borne inoculum has not contributed to the dispersal of *P. ramorum* in Oregon. Most likely infection is establishing in overstory

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tanoak via aerial means and is dispersing locally in rain splash. Importantly, our results support the use of aerial surveys and the detection of deceased, overstory tanoak as a means to describe the distribution of *P. ramorum* in Oregon.

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