Rizzo, D. M. 2003. Sudden Oak Death: Host plants in forest ecosystems in California and Oregon. Sudden Oak Death Online Symposium. www.apsnet.org/online/SOD (website of The American Phytopathological Society). doi:10.1094/SOD-2003-DR

Sudden Oak Death: Host plants in forest ecosystems in California and Oregon

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The symptoms that define Sudden Oak Death were first recognized in 1994-1995. Over the next few years, SOD reached epidemic proportions in oak forests along approximately 300 km of the central California coast. The main hosts included tanoak (*Lithocarpus densiflora*), coast live oak (*Quercus agrifolia*), California black oak (*Q. kelloggii)* and Shreve's oak (*Quercus parvula*var. *shrevei*) (Rizzo et al. 2002). Research into the pathogen soon revealed that *P. ramorum* could infect plant species other than oak and rhododendron (Werres et al., 2001; Rizzo et al, 2002b). Over the past year and a half, an additional 20 plant species from 12 families have been added as hosts for *P. ramorum* throughout its range in California and Oregon forests (Table 1). Additional hosts are likely because many other plant species have been found to be susceptible to infection in laboratory inoculations.

Phytophthora ramorum appears to infect only aboveground plant parts (i.e., leaves, branches, and/or stems). Across the range of hosts, two different types of diseases can be distinguished: non-lethal foliar and twig infections and lethal branch or stem infections (Table 1, Fig. 1). *P. ramorum* causes large cankers on the main stem of oaks and tanoak and may cause tree death. The disease is called 'Sudden Oak Death' because the whole crown of many affected trees appears to die rapidly with the foliage turning from a healthy green to brown over several weeks. However, time from initial infection by *P. ramorum* to tree death may range from several months to several years. A slow decline of infected trees has also been noted, with dieback and reduced size of leaves. Tanoak appears to be the most susceptible species. All size classes of tanoak from seedlings to mature trees may be infected and killed (Rizzo et al. 2002a). Infections on tanoak occur on stems, branches, and leaves. However, on oaks, *P. ramorum* does not appear to infect small branches or leaves as on tanoak; therefore infection and mortality appear to be more commonly associated with larger trees rather than seedlings and saplings. A number of opportunistic organisms are commonly observed on oak and tanoak trees with advanced *P. ramorum* infections including ambrosia beetles (*Monarthrum scutellare* and *M. dentiger*), bark beetles (*Pseudopityophthorus pubipennis*), and a sapwood rotting fungus, *Hypoxylon thouarsianum*. These organisms may hasten the death of *P. ramorum*-infected trees.

Table 1. Known hosts and plant part infected by *Phytophthora ramorum* in.

Host	Common name	Plant part infected and impact
Quercus agrifolia (Fagaceae)	Coast live oak	Stem cankers; death of large trees
Q. kelloggii (Fagaceae)	California black oak	Stem cankers; death of large trees
Q. parvula var. *shrevei* (Fagaceae)	Shreve's oak	Stem cankers; death of large trees
Q. chrysolepsis (Fagaceae)	Canyon live oak	Branch and stem cankers; death of large trees?
Lithocarpus densiflora (Fagaceae)	Tanoak	Stem and branch cankers, foliar lesions; death of large trees, saplings, and regeneration
Arbutus menziesii (Ericaceae)	Madrone	Branch cankers, foliar lesions; death of regeneration and possibly large trees
Vaccinium ovatum (Ericaceae)	Evergreen huckleberry	Stem and branch cankers, foliar lesions; dieback of canes and possible death of plants
Arctostaphylos spp. [1] (Ericaceae)	Manzanita	Stem and branch cankers, foliar lesions; dieback of branches, long-term impact on individual plants unknown
Rhododendron spp.[2] (Ericaceae)	Ornamental rhododendron	Stem and branch cankers, foliar lesions; dieback and death of plants
Umbellularia californica (Lauraceae)	Bay laurel, Oregon myrtle	Foliar lesions; long-term impact on individual plants unknown
Acer macrophyllum (Aceraceae)	Bigleaf maple	Foliar lesions; long-term impact on individual plants unknown
Heteromeles arbutifolia (Rosaceae)	Toyon	Branch cankers, foliar lesions; branch dieback, long-term impact on individual plants unknown
Rubus spectabilis (Rosaceae)	Salmon berry	Foliar lesions; long-term impact on individual plants unknown
Aesculus californica (Hippocastanaceae)	California buckeye	Foliar lesions; long-term impact on individual plants unknown
Rhamnus californica (Rhamnaceae)	Coffeeberry	Foliar lesions; long-term impact on individual plants unknown
Rhamnus purshiana (Rhamnaceae)	cascara	Foliar lesions; long-term impact on individual plants unknown
Corylus cornuta	California	Foliar lesions; long-term

(Betulaceae)	hazelnut	impact on individual plants unknown
Lonicera hispidula (Caprifoliaceae)	Honeysuckle	Foliar lesions; long-term impact on individual plants unknown
Viburnum spp.[3]	Viburnum	Basal stem lesions leading to wilting and death of entire plants
Toxicodendron diversilobum (Anacardiaceae)	Poison oak	Stem cankers
Trientalis latifolia (Primulaceae)	Western starflower	Foliar lesions; long-term impact unknown
Sequoia sempervirens (Taxodiaceae)	Coast redwood	Branch cankers, foliar lesions; death of sprouts, long-term impact on saplings and trees unknown
Pseudotsuga menziesii (Pinaceae)	Douglas-fir	Branch cankers, foliar lesions; death of new shoots and small branches, long-term impact on saplings and trees unknown

[1] Probably multiple species infected. Known definitively from *A. manzanita*.
[2] Multiple species infected including *R. macrophyllum* and *R. catawbiense*.
[3] Multiple species infected including *V. bodnantense*, *V. fragans*, *V. plicatum*, and *V. tinus*. This host only known from Europe.

Despite the wide host range of *P. ramorum*, oaks in the subgenus *Quercus* (i.e., the white oaks) still appear to be unaffected by *P. ramorum* in the field (Rizzo et al., 2002a). Blue oak (*Q. douglasii*) and valley oak (*Q. lobata*), the major oak species of the inner coastal ranges, central valley, and Sierra Nevada foothills of California, fall into the white oak group as does Oregon white oak (*Q. garryana*).

Not enough is known yet about disease progression and the extent of damage on individual plants of most non-oak hosts. On several species in the rhododendron family, *P. ramorum* has been found to cause significant leaf blight and branch dieback (Table 1, Fig. 2). Death of madrone saplings in less than 4 months has been observed in the field, and it is suspected that the pathogen can kill mature madrone trees. Death of mature native rhododendrons has been observed in Oregon (Goheen et al., 2002). Dieback has also been noted on redwood sprouts and Douglas-fir saplings (Davidson et al., 2002; Maloney et al., 2002). On other hosts, such as California bay laurel and bigleaf maple, *P. ramorum* appears to be primarily a leaf pathogen, infecting very few stems (Table 1).

Foliar infections of non-oak hosts may play a key role in the epidemiology of *P. ramorum* at the local scale by serving as a source of inoculum, which is then spread aerially through rainsplash (Davidson et al., 2002a). The most likely dispersal propagules of *P. ramorum*, sporangia and chlamydospores, are readily produced on foliage (particularly bay laurel and

rhododendron), but they have yet to be reported from infected oak bark (Davidson et al., 2002a). It is hypothesized that *P. ramorum* may need to build inoculum on these associated hosts to serve as a springboard to oak species. Even hosts with relatively small lesions may be important in the transmission biology of *P. ramorum* because such lesions do not kill leaves and may support abundant sporulation. Thus, forests with a diversity of plant hosts may be more susceptible to invasion by *P. ramorum*. Two recent studies in California found a significant association between the presence of bay laurel trees and *P. ramorum* infection on oak (Kelly and Meentemeyer, 2002; Swiecki and Bernhardt, 2002). Preliminary studies have found that foliar host infection may precede infection of oak and tanoak on individual sites.

Over its range in coastal California and Oregon, *P. ramorum* is associated with several different forest types at elevations ranging from sea level to over 800 meters (Rizzo et al. 2002). Oaks and tanoak occur in closed-canopy, mixed evergreen forests that can be divided into those with and without a significant component of Douglas-fir. Other major hardwood associates in these mixed evergreen forests include California bay laurel and madrone. In coast redwood forests, an understory of tanoak mixes with a number of shrub species such as rhododendron and evergreen. Nearly all of the woody plant species in these forest types are now confirmed as potential hosts for *P. ramorum*. Hosts for *P. ramorum* include canopy trees, understory shrubs, and at least one herbaceous plant. The long-term consequences in terms of mortality for non-oak hosts are unknown at this time. Sub-lethal infections of non-oak hosts may allow *P. ramorum* to persist indefinitely in infested forests and affect the success of future regeneration and restoration efforts.

Genetic resistance in host populations will also affect spread of the disease. Preliminary studies (Dodd and Garbelotto, unpublished) indicate that individuals of both bay laurel and coast live oak display different levels of resistance to the disease. Determining how this resistance is distributed among populations across the geographic range of these hosts may allow predictions on the spread of the disease.

Of great concern is the potential for the establishment of *P. ramorum* in forests outside of the West Coast. Laboratory inoculations have found that two eastern North American oaks, northern red oak (*Q. rubra*) and pin oak (*Q. palustris*) are susceptible to infection by *P. ramorum* (Rizzo et al. 2002b). Extrapolation of results from seedling experiments to the potential effects on mature trees must be done cautiously. However, because lesion sizes in red oak and pin oak seedlings were much larger than in coast live oak seedlings (a species in which the adults are very susceptible), we suggest that it is likely that mature trees of northern red oak and pin oak will be susceptible to infection by *P. ramorum*. Rhododendron catawbiense, native to the eastern United States, has been found to be infected by *P. ramorum* in nurseries and gardens in Germany (Werres et al. 2001). Because of limited knowledge of the ecology of *P.*

ramorum, the ultimate impact of this pathogen if it became established in new geographic locations is difficult to predict.

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