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Title: Potential Susceptibility of Tanoak Associated and Rare Ericaceous Plant Species of Southwestern Oregon to *Phytophthora ramorum*

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The sudden oak death pathogen, *Phytophthora ramorum*, is present in southwestern Oregon, and while an eradication effort is underway, the potential impact of the polyphagous pathogen on surrounding vegetation is unknown. Plant communities in the area are substantially different from those affected in California, although tanoak (*Lithocarpus densiflorus*), evergreen huckleberry (*Vaccinium ovatum*) and Pacific rhododendron (*Rhododendron macrophyllum*) are hosts found in both areas. Other species are likely to be susceptible to the pathogen. Detached leaf and whole plant assays were used to test species commonly associated with tanoak, as well as three rare or endemic ericaceous species of the western Siskiyou Mountains and their associated taxa. Leaves and plants were challenged with zoospore suspensions that were capable of generating symptoms in the known hosts tanoak and evergreen huckleberry. Most (78%) of the previously unchallenged species developed necrotic lesions in detached leaf assays although severity (% leaf area necrotic) was variable. All three of the ericaceous species of conservation concern: *Arctostaphylos hispidula*, *Kalmiopsis leachiana*, and *Leucothoe davisiae* were susceptible in detached leaf assays. Factors important in determining whether or not these species will become infected in their native habitat are discussed.

Potential Susceptibility of Tanoak Associated and Rare Ericaceous Plant Species of Southwestern Oregon to *Phytophthora ramorum*

by

James W. Zanzot

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

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James W. Zanzot, Author

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Chapter 1. Introduction and literature review

1.1 Sudden oak death and *Phytophthora ramorum*

The disease known as sudden oak death (SOD) was first observed around 1994, when homeowners in Marin County, California (north of San Francisco) began to notice tanoaks (*Lithocarpus densiflorus*) dying on their properties. As reports accumulated, extension agents and university researchers began to take notice. Many causal agents were hypothesized based on consistent observations at oak mortality sites, including ambrosia beetles (*Monarthrum* spp.), bark beetles (*Pseudopityophthorus pubipennis*) and fungi (*Hypoxylon thouarsianum*) (Garbelotto et al. 2001). True oak species, including coast live oak (*Quercus agrifolia*) and California black oak (*Q. kelloggii*) were also dying with symptoms similar to the tanoaks, and residents in other counties began to observe the phenomenon. In June 2000, the causal agent was identified as an unknown species of *Phytophthora* (Rizzo et al. 2002). Subsequent to the identification, several other plant taxa were shown to harbor the pathogen, though observed symptoms were different from oaks (Rizzo et al. 2002b). At present, 12 California counties have confirmed cases of sudden oak death (California Oak Mortality Task Force [COMTF] 2003), and hundreds of thousands of trees have been killed (Rizzo et al. 2002).

In 1993, a new twig blight disease was noted in nurseries in Germany and the Netherlands, affecting ornamental rhododendrons and viburnums. The pathogen et al. 2001), and was also recovered from recirculated irrigation water (Themann et al. 2002). The new species was described as *Phytophthora ramorum* Werres, De Cock and Man in't Veld, the species epithet derived from the Latin word for branch, reflecting the aerial habit of the pathogen (Werres et al. 2001).

Shown cultures of the new European *Phytophthora* and the California *Phytophthora,* mycologist Clive Brasier determined that they were of the same species (Rizzo et al. 2002), though subsequent genetic data revealed they are of different mating types; Europe having the A1 mating type, and the US, A2 (Werres et al 2001, Zielke and Werres 2002).

In August 2001, the Oregon Department of Agriculture (ODA) and Oregon Department of Forestry (ODF) announced that *P. ramorum* had been positively identified from tanoaks in Curry County, near the city of Brookings, in the southwestern corner of the state (Goheen et al. 2002). The location was more than 360 km from the nearest known infestation in Mendocino County, California although a subsequent infestation has been found in Humboldt County, more than 200 km from Brookings. The infected trees were clustered within a nine-square-mile area (which has been quarantined), and the decision to attempt eradication was made (Goheen et al. 2002, Goheen et al 2002b). Infected hosts and surrounding vegetation were cut, piled, burned, and the treated areas broadcast burned. As of September 2003, surveys have found only one infection locus outside the quarantined area, and few new loci within the quarantine area, suggesting that the eradication effort has been effective in limiting disease spread though complete extirpation has yet to be achieved (Kanaskie et al. 2003).

Many European nations have since found infected nursery stock within their borders, including Poland (Orlikowski and Szkuta 2002), France (Delatour et al. 2002), the United Kingdom (UK) (Lane et al. 2003), Spain (Moralejo and Werres 2002), Belgium (DeMerlier et al. 2003), Sweden (COMTF 2003), and Italy (COMTF 2003). In the UK, over 221 sites have been found to have plants infected with *Phytophthora ramorum* (Department for Environmental, Food, and Rural Affairs UK [DEFRA] 2003).

To raise public awareness about the problem in California, managers and researchers formed the California Oak Mortality Task Force (COMTF 2003). Many publications appeared on the agency's website (suddenoakdeath.org) as the disease phenomenon expanded. A symposium dedicated to scientific research on *Phytophthora ramorum* was held in Monterey, CA in December 2002, bringing scientists from Europe, Oregon, California, and other areas together to discuss the biology, pathology, epidemiology, and regulation of the pathogen. Additionally, an online symposium was convened in April 2003 hosted by the American Phytopathological Society (www.apsnet.org) and drawing the broader community of plant pathologists.

In May 2003, ODA announced that *Phytophthora ramorum* had been positively identified from a nursery in Clackamas County, at the northern end of the state near Portland. Infected plant taxa included viburnum *(Viburnum* X *bodnantense* and *Viburnum plicatum tomentosum)*, andromeda (*Pieris japonica*) and rhododendron (*Rhododendron* hybrid 'Unique') (Osterbauer et al. 2003). Infected plants were destroyed. Subsequent tests have revealed that some of the Clackamas isolates are of the same mating type as the European isolates (Osterbauer et al 2003, Hansen et al. in press).

On 5 June 2003, the Washington State Department of Agriculture (WSDA) announced the presence of the SOD pathogen on nursery stock found in southern King County, near Seattle (WSDA 2003) in a sister nursery to the one in Clackamas County. Shortly thereafter, on 13 June 2003, the Canadian Food Inspection Agency (CFIA) announced that *P. ramorum* had been found on rhododendrons in a nursery in British Columbia (CFIA, 2003). Infected camellias (*Camellia sasanqua*) were also found in southern Oregon at garden centers in Ashland and Medford. The camellias were infected with the A2 mating type, and were traced back to a nursery in Stanislaus County, CA (an officially uninfested county). The finding was made shortly after British inspectors had discovered *P. ramorum* on camellias in the UK. Some Stanislaus County camellias had been shipped to retail centers in the Portland area and had been sold and a recall was issued. Approximately 100 of 300 camellias sold have been traced in the recall, and only one of these was infected (N.K. Osterbauer, personal communication). All known infected plants in Oregon have been destroyed (Osterbauer et al. 2003).

1.2 *Phytophthora ramorum* in context

1.2.1 *Phytophthora*, the plant destroyer

With rare exception, all members of the genus *Phytophthora* are plant pathogens (Erwin and Ribeiro 1996). At least 60 species exist (Erwin and Ribeiro 1996), and many additional species have been described (e.g. Jung et al. 2002, Werres et al. 2001, Davidson et al. 2002c). Exemplar species include: *P. infestans*, which causes late blight of potato, central to the Irish Potato Famine of the mid-1800's, *P. lateralis*, cause of Port-Orford-cedar root disease (reviewed in section 1.6.2 below), and *P. cinnamomi*, which causes several diseases including avocado root rot, littleleaf disease of southeastern pines, and the jarrah dieback of Western Australia (reviewed in section 1.6.1 below).

Phytophthora are oomycetes, which are not true fungi (i.e., of the kingdom Myceteae). Like true fungi, they form mycelia, absorb their nutrition from their environment, and reproduce by spores, but they are more closely related taxonomically to brown algae and have been considered to be in the kingdom Chromista (Cavalier-Smith 1986), Stramenopiles (Patterson 1989), or Protoctista (Dick 1990), depending on the author and context. Several types of spores are produced. Sporangia may be shed as infective propagules and may germinate directly or release zoospores. Zoospores are biflagellate motile cells that swim through free water to plant surfaces. Chlamydospores are thought to be survival structures for withstanding times of environmental hardship, as are oospores, the latter of which are the product of sexual recombination (Erwin and Ribeiro 1996). Being heterothallic, and having the two mating types geographically separated in Europe and the U.S. until recently (Osterbauer et al. 2003), *P. ramorum* has only been observed to produce oospores under laboratory conditions (Werres et al. 2001, Werres and Zielke 2003, Reeser et al., in press).

1.2.2 Host range

P. ramorum, at present, has been observed to infect 23 plant species in the Fagaceae, Ericaceae, Rhamnaceae, Caprifoliaceae, Rosaceae, Pinaceae and six other families (see table 1.1) (Davidson et al. 2003). Symptoms manifest themselves in different ways depending on the host, prompting researchers to suggest that *P. ramorum* causes three different diseases depending on the species being infected: sudden oak death, ramorum shoot dieback, and ramorum leaf blight (Hansen et al. 2002b). Red oaks (*Quercus* subsection Erythrobalanus) and tanoak (*Lithocarpus densiflorus*) experience sudden oak death; ericaceous hosts, some conifers and young tanoak develop ramorum shoot dieback; and many other taxa, ramorum leaf blight (see section 1.2.3 for descriptions of symptoms below).

It also appears that oaks are not the main hosts for the pathogen, only the most susceptible and possibly terminal hosts. Other hosts, such as Oregon myrtlewood/California bay laurel (*Umbellularia californica)* may show few symptoms, but generate large amounts of inoculum (Garbelotto et al. 2003). In Oregon, although *U. californica* is present near infected tanoaks, the pathogen has been recovered from myrtlewood only once. New hosts have been discovered in Oregon also: cascara (*Rhamnus purshiana*), poison-oak (*Toxicodendron diversilobum*), and salmonberry (*Rubus spectabilis*) (Goheen et al. 2002d).

1.2.3 Symptoms

On SOD hosts, the most distinctive symptoms are bleeding lesions on the main stem that do not extend below the root collar, but may be high up on the bole (Rizzo et al. 2002). Beneath the bark, reddish or brown, dark margined lesions are present. Shoots may wilt forming "shepherd's crooks", and occasionally, leaves may have necrotic lesions. "Sudden oak death" occurs when green trees undergo a complete browning in less than a month, though these trees may have been infected for over a year before the precipitous decline (Davidson et al. 2003).

Table 1.1 List of naturally infected hosts for *Phytophthora ramorum*

Species	Common name	Family	Location	Notes	Source
Abies grandis	Grand fir	Pinaceae	CA	In Christmas tree plantation	COMTF 2003
Acer macrophyllum	Bigleaf maple	Aceraceae	CA		Rizzo et al. 2002b
Aesculus californicus	California buckeye	Hippocastanaceae	CA		Rizzo et al. 2002b
Arbutus menziesii	Madrone	Ericaceae	CA		Rizzo et al. 2002b
Arbutus unedo	Strawberry tree	Ericaceae	Spain		COMTF 2003
Arctostaphylos manzanita	Manzanita	Ericaceae	CA	Only PCR, no culture	Rizzo et al 2002b
Camellia spp.		Theaceae	CA, OR, UK	*C. sasanqua* 'Bonanza'	A. Inman, pers. comm. Osterbauer et al. 2003
Heteromeles arbutifolia	Toyon	Rosaceae	CA		Rizzo et al. 2002b
Kalmia latifolia	Mountain laurel	Ericaceae	UK		COMTF 2003
Lithocarpus densiflorus	Tanoak	Fagaceae	CA, OR	Only var. *densiflorus*	Rizzo et al. 2002, Goheen et al 2002.
Lonicera hispidula	Hairy honeysuckle	Caprifoliaceae	CA		Rizzo et al. 2002b
Pieris spp.	Andromeda, pieris	Ericaceae	UK, OR	*P. japonica* 'Forest Flame', *P.* X 'Brouwer's Beauty'	Osterbauer et al. 2003
Pseudotsuga menziesii	Douglas-fir	Pinaceae	CA	New growth on juveniles	Davidson et al. 2002b

Table 1.1 List of naturally infected hosts for *Phytophthora ramorum* (continued)

Species	Common name	Family	Location	Notes	Source
Quercus agrifolia	Coast live oak	Fagaceae	CA		Garbelotto et al. 2001
Q. chrysolepis	Canyon live oak	Fagaceae	CA	Only location: Mt. Tamalpais, CA	Murphy and Rizzo 2002
Q. kelloggii	California black oak	Fagaceae	CA		Garbelotto et al. 2001
Q. parvula var. *shrevei*	Shreve's oak	Fagaceae	CA	Only 1 individual	Garbelotto et al. 2001
Rhamnus californica	California coffeeberry	Rhamnaceae	CA		Rizzo et al. 2002b
Rhamnus purshiana	Cascara	Rhamnaceae	OR		Goheen et al. 2002c
Rhododendron macrophyllum	Pacific rhododendron	Ericaceae	CA, OR		Goheen et al. 2002, Rizzo et al. 2002b
Rhododendron spp.	Ornamental rhododendron	Ericaceae	CA, OR, EU	Several cultivars	Werres et al. 2001, Osterbauer et al. 2003
Rubus spectabilis	Salmonberry	Rosaceae	OR	In forests near Brookings	Goheen et al. 2002c
Sequoia sempervirens	Coast redwood	Taxodiaceae	CA		Maloney et al. 2002
Taxus baccata	Yew	Taxaceae	UK		COMTF 2003
Toxicodendron diversilobum	Poison-oak	Anacardiaceae	OR, CA		Goheen et al. 2002c

Table 1.1 List of naturally infected hosts for *Phytophthora ramorum*(concluded)

Species	Common name	Family	Location	Notes	Source
Trientalis latifolia	Western starflower	Primulaceae	CA		Huberli et al. 2003
Umbellularia californica	Oregon myrtlewood/ California bay laurel	Lauraceae	CA*		Rizzo et al. 2002b, Goheen et al. 2002c
Vaccinium ovatum	Evergreen huckleberry	Ericaceae	CA, OR		Rizzo et al. 2002b, Goheen et al. 2002
Viburnum spp.	Viburnum	Caprifoliaceae	EU, OR	*V.* X *bodnantense, V. plicatum tomentosum* 'Mariesii',	Werres et al. 2001, Osterbauer et al. 2003

* one infected individual has been found in Oregon which has been destroyed

The one true oak host not of the red oak subsection, canyon live oak (*Quercus chrysolepis,* subsection Protobalanus), exhibits dieback but it is not known whether it may be killed in the field (Murphy and Rizzo 2003). The pathogen was recovered from an individual shrub, and thus it is not currently known if the tree form may be infected. The case is similar for conifer hosts such as coast redwood (*Sequoia sempervirens*) (Maloney et al. 2002) and Douglas-fir (*Pseudotsuga menziesii*) (Davidson et al. 2002); few individuals have been found to be infected, and those infected are not known to be killed. Stems may die back, but damage to mature trees is not evident. These symptoms are characteristic of ramorum shoot dieback, and are evident in many members of the Ericaceae. In several ericaceous hosts, including *Arbutus menziesii*, *Rhododendron macrophyllum*, and *Vaccinium ovatum*, the dieback may be fatal to the plant (Davidson et al. 2003).

On foliar hosts, necrotic lesions may differ in appearance. The lesions may appear as spots (e.g. *Aesculus californica*), scorch (e.g. *Acer macrophyllum*) or spreading lesions on any portion of the leaf, most typically where moisture accumulates (e.g. *Umbellularia californica*) (Rizzo et al. 2002b, Davidson et al. 2003). It is less certain whether any of these foliar hosts may be killed, but an understanding of their role in the epidemiology of the disease is evolving (Garbelotto et al. 2003).

1.3 Tanoak and tanoak associations

Tanoak, also known as tanbark oak, *Lithocarpus densiflorus* (Hook and Arn.) Rehd., is phyletically distinct from the genus of true oaks, *Quercus*, though both taxa produce acorns. Tanoak was originally described as *Quercus densiflorus* (Tucker 1980), due to fruit morphology, though the scales on the cup of a tanoak acorn are distinct from oak; phylogenetic analysis supports the distinction (Manos et al. 2001). The genus is most widely distributed throughout southeastern Asia. *L. densiflorus* sensu lato is the sole representative of the genus in North America, and shares an ancestor with the genus *Chrysolepis* (western chinquapins) rather than Asian *Lithocarpus* (Manos et al 2001). Two varieties of the American species are recognized, *L. densiflorus* var. *densiflorus*, which may grow into a tree up to 80 m tall, and *L. densiflorus* var. *echinoides*, which is a shrub, and has wavier leaf margins (Hickman 1993). Both are endemic to the California floristic province, which includes the Klamath ranges extending into southwestern Oregon (Siskiyou Mountains). The shrubby variety is found at the northern and eastern ends of the species range on lower quality ("sterile" Peck 1961) sites; dry sites or on rocky or low nutrient soils such as serpentine.

Tanoak's value in human terms has shifted greatly in the past 150 years (McDonald and Tappeiner 1987). Tanoak acorns have been and continue to be consumed by indigenous people in California and Oregon (Roy 1957, McMurray 1989). Tanoak produces acorns more copiously than any California *Quercus* species (in Roy 1957). The bark was once harvested for tannins, used in leather production and inspiring the common name (McMurray 1989). As source of wood and commercial value, the literature is at odds. Tanoak wood is comparable in strength to other oaks, though is not widely used because of limited supply (Immel 2002). Others agree on the strength and overall quality of the timber, but suggest that it doesn't compare in value with conifer production, and often competes with more valuable conifers in natural forests. Thus it is construed as a weedy species (McDonald and Tappeiner 1987). Previous authors have described tanoak as an undesirable forest species or downplayed the importance of tanoak in forests of northwestern California and southwestern Oregon (Bolsinger 1988, Franklin and Dyrness 1988). A Forest Service report described an "unusual dieback of tanoak sprouts", a disease which affects tanoak resprouts. The authors suggested the potential for use as a biocontrol agent for suppressing tanoak after conifer harvest (McDonald et al. 1988). (N.B. the symptoms described do not match those observed in SOD).

Several other hardwood species, including many sclerophylls, are associated with tanoak including madrone (*Arbutus menziesii*), Oregon myrtlewood (California bay laurel) (*Umbellularia californica*), red alder (*Alnus rubra*), and bigleaf maple (*Acer macrophyllum*). These species, in many different combinations correlated with climatic and site differences, often flourish after timber harvest, and thus are considered weedy (Bolsinger 1988).

The native range of tanoak extends from near Coos Bay, Oregon, south to near Santa Barbara, California. Often found in areas with coastal influence, tanoak is present in redwood (*Sequoia sempervirens*) forests, mixed with Douglas-fir (*Pseudotsuga menziesii*), in mixed-sclerophyll forests, or in stands where it forms a closed canopy (McMurray 1989). Tanoak may also be found in stands with Port-Orford-cedar (*Chamaecyparis lawsoniana*) (Atzet et al. 1996).

In northwestern California and southwestern Oregon, many areas with a coastal influence have at least a nominal cover of tanoak, and the tree may be present in dense stands (Franklin and Dyrness 1988, Atzet et al. 1996, Jimerson et al. 1996). Ecologists describing the forests of the area have previously lumped tanoak with other hardwoods in a mixed-evergreen (*Pseudotsuga*-sclerophyll) zone (Franklin and Dyrness 1988). They note that Douglas-fir and tanoak are the two most important tree species. Subsequent ecological studies by Forest Service ecologists on both sides of the western Oregon-California state line (Atzet et al. 1996, Jimerson et al. 1996) describe many community types where tanoak is the projected climax species. In their assessments, tanoak is the only hardwood species other than Oregon white oak (*Quercus garryana*, a much less abundant and diverse forest type) to rank as a climax species (Atzet et al. 1996).

Towards the coast, common understory species associated with tanoak include salal (*Gaultheria shallon*), dwarf Oregon-grape (*Berberis nervosa*), western swordfern (*Polystichum munitum*), evergreen huckleberry (*Vaccinium ovatum*) and Pacific rhododendron (*Rhododendron macrophyllum*). In drier areas, other understory species become abundant, including manzanita (*Arctostaphylos* spp.) and hairy honeysuckle (*Lonicera hispidula*) as well as drought-tolerant trees such as California black oak (*Quercus kelloggii*) and Oregon white oak (*Q. garryana*).

The areas affected by *Phytophthora ramorum* in southwestern Oregon are substantially different from those found in tanoak communities in California, being over 200 km north of the Humboldt County, CA infestation. None of the tanoak infestations in Oregon occur with coast redwood (*Sequoia sempervirens*). Researchers in California describe *P. ramorum* as being found in "cool areas", in Oregon the pathogen has been found in some of the warmest tanoak associations (see Figure1.1). And while many hosts from California are also present in Oregon, most have not yet been infected, and, as previously noted, new hosts have been found. Poison-oak (*Toxicodendron diversilobum*) has subsequently been identified as a host in California as well (Davidson et al. 2003).

1.4 Rare and endemic plant taxa of the Siskiyou Mountains

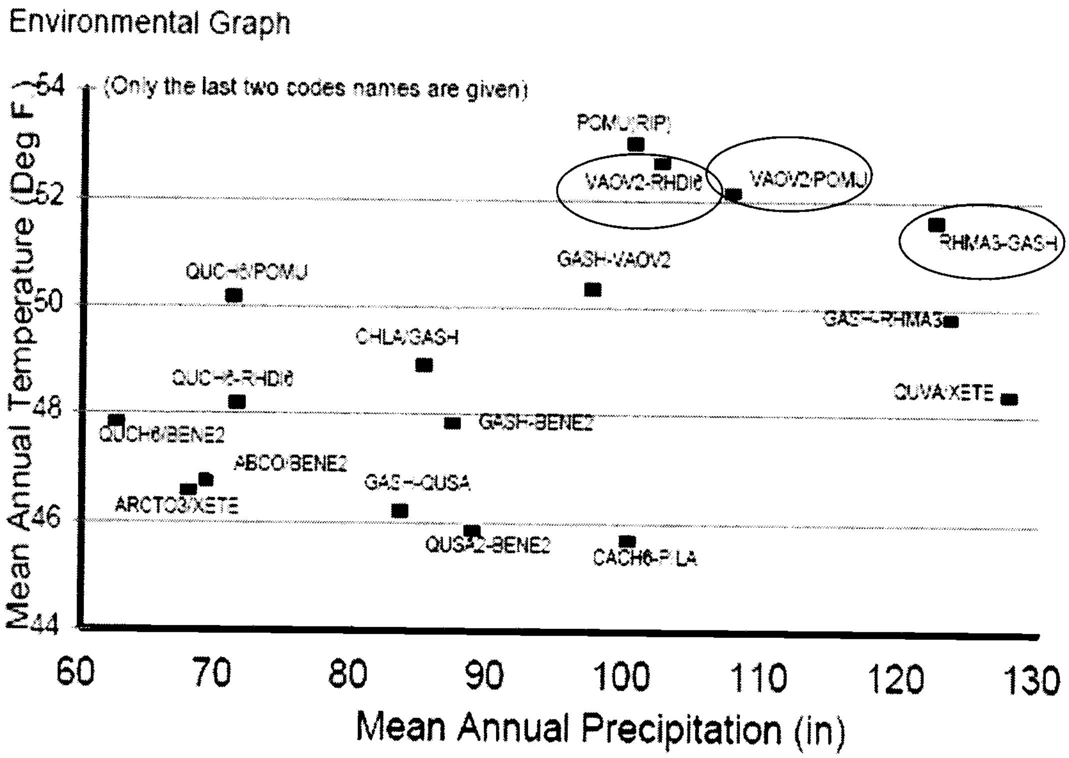
The Siskiyou Mountains of southwestern Oregon and northwestern California are the northernmost of the Klamath Ranges. The Klamaths are considered to be the nexus of the California Floristic Province and the Northwestern flora and are an "area of exceptional ecological interest" (Whittaker 1960, p. 279). The area is geologically, topographically, and climatically complex. The Klamaths are much older than the surrounding landmasses, and have been refugia during periods of glaciation. All of these factors have contributed to superlative plant species richness and endemism (Whittaker 1960, Stebbins and Major 1965).

Subsequent studies suggest that while some species are relict (paleoendemics) many of the endemic plant taxa are derived from more widespread parent species that have specialized (neoendemism), on serpentine, for example (Smith and Sawyer 1988). Three rare ericaceous species are considered in this study; a paleoendemic (*Kalmiopsis leachiana*), a neoendemic (*Arctostaphylos hispidula*), and a species not endemic to the Siskiyous (*Leucothoe davisiae*). This relationship is fortuitous, and is not considered further in this thesis. Their biologies are briefly noted here.

1.4.1. *Arctostaphylos hispidula* Howell.

The genus *Arctostaphylos* (Greek; bear-berry) is the most diverse genus of shrubs in the California Floristic Province (Wells 2000) with 110 species, subspecies and varieties (CalFlora 2000). The genus is notorious for rampant hybridization and introgression, generating many subspecies and varieties (Wells 2000). Many locally adapted, rare, endemic taxa exist, including the "rarest plant in the world", Presidio manzanita (*A.*

Figure 1.1. Tanoak associations of southwestern Oregon (from Atzet et al. 1996). Each data point represents an association where tanoak (*Lithocarpus densiflorus*) is dominant. Ovals (added by the author) indicate where *Phytophthora ramorum* has been found.



Key: ABCO= *Abies concolor*, ARCTO= *Arctostaphylos* spp., BENE2= *Berberis nervosa*, CACH6= *Chrysolepis chrysophylla*, CHLA= *Chamaecyparis lawsoniana*, GASH= *Gaultheria shallon*, PILA= *Pinus lambertiana*, POMU= *Polystichum munitum*, QUCH= *Quercus chrysolepis*, QUSA= *Quercus sadleriana*, QUVA= *Quercus vaccinifolia*, RHDI6= *Toxicodendron diversilobum*, RHMA3= *Rhododendron macrophyllum*, VAOV2= *Vaccinium ovatum*, XETE= *Xerophyllum tenax* *hookeri* ssp. *ravenii*) of which only one genet is known (Skinner and Pavlik 1994). Currently, 60 rare taxa are recognized by the California Native Plant Society (CNPS) (Skinner and Pavlik 1994).

CNPS had placed *A. hispidula* on list 3 ("rare but not endangered", Smith et al. 1980) though presently it is on list 4 ("plants of limited distribution", Skinner and Pavlik 1994). Also, a qualification of the list assignment is employed, the Rareness-Endangerment-Distribution (RED) code, and is given a RED score of 1-2-2, meaning the taxon is Rare, but widely distributed in CA ('least rare' on the 1-3 scale), it's Endangered in a portion of its range, and its Distribution is rare outside of California (Skinner and Pavlik 1994).

The Oregon Natural Heritage Program (ONHP) also monitors *A. hispidula*, which is Oregon's only rare manzanita. Since the plant is much less abundant, *A. hispidula* is on list 2 in Oregon ("threatened, endangered or extirpated from Oregon, secure elsewhere"). They also assign a heritage rank of G3 S2, meaning globally, the species is rare, uncommon or threatened, though not imperiled (21-100 occurrences), and within the state, the species may be imperiled due to rarity or other factors (6-20 occurrences) (ONHP 2001).

The plant is typically an erect shrub less than 2 m (Hickman 1993), though on harsher sites the plant may be prostrate, and difficult to tell from a common associate, *A. nevadensis* (Bouldin 1992) (see Figures 1.2 and 1.3). The leaves are isofacial, oblanceolate to elliptic, 1.5-3 cm long by 0.5-1.5 cm wide (Hickman 1993), and have a scabrous (sandpapery) texture that is an important field identification characteristic

(Mullens 2000) though only *A. patula* may be confused for *A. hispidula* in its native range except as previously noted (Bouldin 1992). The plant has no burl or lignotuber, the organ that allows for resprout after fire, and thus the plant relies on seed germination to reestablish after fire (Bouldin 1992). *A. hispidula* is found typically on dry rocky ridges, often on serpentine, though occasionally on sandstone (Peck 1961, Bouldin 1992).

The majority of populations of *A. hispidula*, some quite large, are in Del Norte County, California, in the Smith River National Recreation Area, with populations in Oregon ranging from Ninemile Spring, on the shared border of Curry, Josephine and Douglas counties at the northern extreme, near Takilma in the Illinois Valley at the easternmost confirmed extreme, and nearly to the Pacific Ocean.

Disjunct populations are found in northern Humboldt County, CA, and two small populations in northern Sonoma County, CA (Bouldin 1992).

1.4.2. *Kalmiopsis leachiana* (Hend.) Rehd.

Lilla Leach discovered this plant in southwestern Oregon in 1930 (Love 1991). Recognizing its novelty to science, Mrs. Leach submitted dried specimens to the University of Oregon Herbarium, where Louis Henderson described the species as a new species of *Rhododendron, R. leachianum*. Rehder, at Harvard, later revised the diagnosis of Henderson, erecting the new genus, *Kalmiopsis*, for its resemblance to *Kalmia* (though they are not closely related [Kron 1997]) and the single species named for the discoverer. Populations have also been found in the North Umpqua River Watershed, which were originally thought to be of the same species as those present in the Siskiyous, though currently they are considered to be a separate species, *Kalmiopsis fragrans*

Figure 1.2 A fruiting branch of *Arctostaphylos hispidula*, on Mount Emily

Figure 1.3 *Arctostaphylos hispidula* (foreground) and its common associate *A. columbiana* (background, lighter green), on Palmer Butte

(Meinke and Kaye, in perp.), having a different substrate preference, flower morphology, and fragrance (T.N. Kaye, personal communication). The North Umpqua kalmiopsis (*K. fragrans*) is much more limited in distribution (ONHP 2001). *K. fragrans* is on ONHP's list 1 (most rare), while *K. leachiana* is on list 4 (ONHP 2001).

Kalmiopsis sensu lato is a low shrub under 2.5 dm, copiously branched. The many elliptic-obovate leaves bear distinctive golden glands on the abaxial surface. The flowers are regular, pink to deep rose and are distylous, a trait unique to *Kalmiopsis* within the Ericaceae (Peck 1961, Marquis 1978)(Figures 1.3 and 1.4).

The ecology and distribution of *K. leachiana* has been studied extensively in a master's thesis by R.J. Marquis (1978). Three main habitat types are described; high and low Siskiyou habitats, and Cascades (North Umpqua) habitat. Low elevation sites (300 to 600 m) have the greatest species diversity, with a conifer layer dominated by *Pseudotsuga menziesii* and *Pinus lambertiana*, a lower sclerophyll layer principally containing *Lithocarpus densiflorus* var. *densiflorus* and *Quercus chrysolepis*, and an evergreen shrub layer dominated by *Vaccinium ovatum*, *K. leachiana*, and *Gaultheria shallon* (Marquis 1978).

At high elevation sites (> 900 m), the shrubby variety of tanoak, *L. d.* var. *echinoides* is prevalent, as is *Q. vaccinifolia*, also a shrub. Both replace their generic counterparts. Also present are a number of other evergreen shrubs, including: *Rhododendron macrophyllum, Q. sadleriana, Arctostaphylos canescens*, and *Vaccinium parvifolium*.

K. leachiana sensu stricto is found only in the Upper Chetco and Lower Illinois River drainages, within 60 km of the Pacific Ocean in the Siskiyou Mountains. With one known exception, all populations are found in the Kalmiopsis Wilderness, nested within Siskiyou National Forest.

While the focus of this study is the potential impact of *P. ramorum*, it should be noted that another, unknown agent is causing mortality on some populations of *K. leachiana* in the Wilderness (M. Ulloa-Cruz, personal communication).

1.4.3. *Leucothoe davisiae* Torrey

Leucothoe davisiae, commonly known as Sierra-laurel, is the sole representative of its genus native to the western United States. Estimates of the size of the genus range from 8 to 50 species, depending on whether the source is of a botanical bent (Mabberley 1997), or horticultural (Brickell and Zuk 1997). Among the propagated ornamental species are: *L. axillaris, L. fontanesiana, L. keiskei,* and *L. racemosa. L. davisiae* is also cultivated, which mitigates any danger of extinction due to disease in the broad sense, but certainly merits study, as natural populations represent a genetic repository for the horticulturalist.

Natural populations of *L. davisiae* are at their northernmost in the Siskiyous, and predominantly in Josephine County (on USDI-Bureau of Land Management [BLM] Medford Resource Area and Galice Ranger District, Siskiyou National Forest), though the westernmost known population is on the Gold Beach Ranger District of the Siskiyou National Forest, within 36 km of the Pacific Ocean. All other known populations are found in the Sierra Nevada in California (CalFlora, 2002), from which the plant derives

Figure 1.4 *Kalmiopsis leachiana* in bloom, Kalmiopsis Wilderness, Chetco Ranger District, Siskiyou National Forest

Figure 1.5 *Kalmiopsis leachiana* growing next to *Lithocarpus densiflorus*, Kalmiopsis Wilderness, Chetco Ranger District, Siskiyou National Forest

half of its common name ("laurels" appear in several families, including the Lauraceae and other genera of the Ericaceae such as *Kalmia* [Mabberley 1997]). *L. davisiae* is typically found in boggy or wet areas (Peck 1961, Hickman 1993). In the Siskiyous, *L. davisiae* is often associated with Port-Orford-cedar (*Chamaecyparis lawsoniana*) in the highest elevation populations of the latter species (Zobel et al. 1985, Atzet et al. 1996). Both species prefer mesic habitats, and they typically co-occur in riparian areas or on sites with a perched water table.

The plant is a shrub under 1.5 m with stiff oblong-elliptic leaves. It produces many-flowered racemes of white, urn-shaped flowers (Peck 1961) (Figures 1.5 and 1.6)

Several populations are in the ONHP database, which gives the taxon a heritage rank of G4 S3, meaning globally the plant is not apparently rare or insecure, though possibly so in the long term with >100 occurrences, and within the state, the taxon is rare, uncommon or threatened, but not immediately imperiled (similar to global ranking for *A. hispidula*) (ONHP 2001).

1.5 Pathogens in ecosystems.

Harper (1977) is often considered the first ecologist to consider the importance of pathogens in ecosystems, placing them on an equal footing with herbivores as agents in the development of plant populations and communities. In his tome on plant population biology, he writes "… pathogens appear as an appendix to a rather generous allocation of space to predators. The order could just as well have been reversed." (Harper 1977, p. 483).

Dinoor and Eshed (1984) list several reasons why pathologists should reciprocate, considering native ecosystems. Besides mycological curiosity, native ecosystems are the source of agricultural plant pathogens and other pests, and thus are instructive in the search for resistance genes and other mechanisms of control.

Burdon (1987) applied the principles of plant pathology to population biology, drawing upon examples from agricultural pathology when necessary, and a number of other important reviews have emerged on many aspects of pathogens' influence on natural plant populations including: the evolution of pathogen aggressiveness (Jarosz and Davelos 1995), long term effects on plant community structure (Dickman 1992, Gilbert 2002), the effects of plant pathogens on plant diversity (Alexander 1992, Hansen 1999) and the effects of plant communities on pathogen populations (Burdon 1992).

Dickman (1989) considered several pathosystems (including *P. cinnamomi* in Australia, described below) to posit the long-term effects of pathogens in ecosystems. He notes important criteria that influence how a pathogen may affect long-term ecosystem change: host range (narrow vs. broad), native vs. introduced (or, native and recurrent vs. native in a changing environment vs. introduced), dispersal (wind, water, soil, vectored; long distance vs. short distance), persistence (long lived vs. ephemeral), and environmental effects (directional vs. cyclical, natural vs. anthropogenic). Hansen (1999) reinforces the importance of delineating between native and exotic pathogens in environmental effects. But even with the disparity between native and exotic, the effects on diversity are not simple, as evident in the two *Phytophthora* species now considered.

Figure 1.6 A flowering branch of *Leucothoe davisiae*, near Flat Top, Galice Ranger District, Siskiyou National Forest.

Figure 1.7 *Leucothoe davisiae* near Flat Top, Galice Ranger District, Siskiyou National Forest

1.6 Forest diseases caused by exotic *Phytophthora* species

Besides the many diseases of agricultural commodities, the genus *Phytophthora* causes many diseases in forests throughout the world (Erwin and Ribeiro 1996), and is implicated in grander forest declines (Jung et al. 2002). Two of the most notable species are discussed here: *Phytophthora cinnamomi* and *P. lateralis*. As introduced forest pathogens, their mention here is germane for several reasons; the former for its polyphagous habit, and the latter for its presence in the area of interest (the Siskiyou Mountains) and for its genetic similarity to *P. ramorum*.

1.6.1 *Phytophthora cinnamomi*

Phytophthora cinnamomi is thought to be native to the Malesian archipelago but has since been widely introduced into many new tropical, subtropical, and moderate temperate areas (Zentmyer 1980). *P. cinnamomi* is the benchmark for introduced, polyphagous plant pathogens, causing disease on no fewer than 950 species (Zentmyer 1980). The pathogen causes disease on a number of important commodities including avocado, pineapple, and rhododendrons. In addition to its importance to agriculture, the oomycete has been implicated in many ecosystems where it has been introduced. Littleleaf disease of shortleaf pine (*Pinus echinata*) is attributed to the pathogen in the southeastern United States, as well as a decline of chestnut (*Castanea dentata*) that preceded the more famous chestnut blight caused by *Cryphonectria parasitica* in that area (Crandall et al. 1945). Hansen (1999) notes that with littleleaf disease, the effect on the forest was to increase species diversity in the overstory; as shortleaf pine was eliminated, other species were able to establish.

Also in the Fagaceae, several oak species may be affected by *P. cinnamomi*, e.g.: *Quercus suber* and *Q. ilex* in the Iberian Peninsula (Brasier et al. 1993), *Q. glaucoides*, *Q. peduncularis*, and *Q. salicifolia* in Mexico (Tainter et al. 2000), and *Q. agrifolia* and *Q. suber* in California (Mircetich et al. 1977).

The area where *P. cinnamomi* has been most devastating is in Australia, where eucalypt forests and heathlands been dramatically impacted, with 75% of species being killed on some sites (Weste and Marks 1987). In 1975, it was estimated that 282,000 ha of *Eucalyptus marginata* (jarrah) forests in western Australia had been affected, and disease spreading at a rate of 20,000 ha $year^{-1}$ (in Weste and Marks 1987). Forests in eastern Australia and Tasmania are also infested, and many national parks also, including: the Brisbane Ranges, Wilson's Promontory, the Stirling Ranges, Le Grand, and the Grampians. In the last of these, a long-term (24-year) study monitored changes in vegetation in infested and uninfested areas (Weste et al. 2002). Several susceptible species disappeared from the plots while the pathogen was active, only to return slowly when the pathogen was no long recovered. The implications for rare, endangered and endemic species were still considered grave, and the effect on diversity very much the opposite of the situation in littleleaf disease.

The disease phenomenon has been listed as a "key threatening process" under Australia's Environment Protection and Biodiversity Conservation Act 1999 (Commonwealth of Australia 1999). This same report includes a list that is "not inclusive" of 31 plant taxa in western Australia that are "threatened" and 39 taxa that are "possibly threatened" by *Phytophthora cinnamomi* (Commonwealth of Australia 1999).

The pathogen also threatens rare species in other parts of Australia, including the Brisbane Ranges (Peters and Weste 1997) and Tasmania. Barker (1994) artificially inoculated 47 rare Tasmanian species, and found 36 to be susceptible. In addition, management plans for conservation of these species are proposed using criteria such as population size, landscape position (higher areas being better than low areas), and accessibility by possible vectors such as vehicles and hikers.

Other management strategies have been attempted in Australia including: local eradication, quarantine, sanitation, biological control with antagonistic organisms, and chemical control with phosphites (Commonwealth of Australia 1999).

1.6.2 *Phytophthora lateralis*

Port-Orford-cedar (POC) (*Chamaecyparis lawsoniana*) is an important timber tree native to the Siskiyous (Zobel et al. 1985), and a widely planted ornamental tree. In 1923, a disease affecting POC was observed in nurseries in Washington state, though its causal agent was not identified until 1942 as a new species, *Phytophthora lateralis* (Tucker and Milbraith 1942), so named for the distinctive lateral arrangement of the chlamydospores. The disease was first reported in the native range of POC in 1952 (Roth et al. 1957), and it has since radiated into many native populations of the tree, killing them rapidly.

Like *P. cinnamomi* and most *Phytophthora* species, *P. lateralis* is a root pathogen. Unlike *P. cinnamomi*, *P. lateralis* has a narrow host range. In the Siskiyous, Pacific yew (*Taxus brevifolia*) is the only other naturally infected species (DeNitto and Kliejunas 1991), and only on sites where POC is present and conditions favorable (Murray and

Hansen 1997). Effects on diversity are also dependent on site variables. In areas where POC grows with other conifer species, death of POC frees resources for the other conifer species, and overall forest composition is not greatly altered. In areas where stands of pure POC exist, root disease can change the community to a much greater extent.

Management of POC root disease has several facets. The role of flowing water and movement of infested soil in spreading disease has been established, which has spurred efforts to regulate human and animal traffic by activities such as road and trail closures, and washing of vehicles (Hansen et al. 2000). Additionally, water used for fire suppression is treated to kill any zoospores (E.M. Goheen, personal communication).

Another approach to combating root disease is POC resistance breeding. Genetic disease resistance has been demonstrated (Hansen et al. 1989), and the US Forest Service has supported efforts to selectively breed resistant POC.

Phytophthora ramorum is most closely related to *P. lateralis* based on internal transcribed spacer (ITS) and cytochrome oxidase II (COX 2) sequence data (Werres et al. 2001, Martin et al. 2002). However, many morphological and behavioral characters differ in the two species. *P. ramorum* is heterothallic, with semi-papillate sporangia, has a broad host range, and infects aerial tissues. *P. lateralis* is homothallic, with non-papillate sporangia, has a narrow host range, and infects roots.

1.7 Bioassays to determine host susceptibility

Bioassays, the use of organisms to test the relative infectivity of a pathogen (Agrios 1997), are common in plant pathology. In this study, detached leaves and cultivated plants are being used to test the potential susceptibility of those species in the field.

Often, plant parts act as surrogates for testing whole plant response. Whole plants are expensive, require space, time, and care, and in the case of many wild species, may not be conducive to propagation. Amongst other benefits, using tissues in isolation allows for careful management of the disease organism, which is important for quarantined pathogens such as *P. ramorum*, and also allows for greater control over conditions such as humidity and temperature.

Bioassays are artificial, and as such may give spurious results. Dorrance and Inglis (1997) compared screening methods for assessing foliar resistance to *P. infestans*, causal in potato late blight. Comparing detached leaves, leaf disks, and greenhouse grown plants, they found that detached leaf assays are a helpful, though imperfect tool for partial resistance screening. However, no method is perfect, as even field trials give variable results due to environmental and cultural conditions.

Since the discovery and description of *P. ramorum*, many researchers have been investigating the potential host range of the pathogen using artificial inoculations. Most studied are the species in the families in which most of the known hosts are found: Fagaceae and Ericaceae (Delatour et al. 2002, Inman et al. 2002, Linderman et al. 2002, Moralejo and Hernandez 2002, Parke et al. 2002, Tooley and Englander 2002).

A variety of plant tissues have been tested: leaves, stems, logs, and whole plants. Roots, though important in most other *Phytophthora* diseases, have not been widely studied as avenues of infection for *P. ramorum*, as the primary in situ studies have found no infection on roots (Werres et al. 2001, Rizzo et al. 2002).

Most researchers have used mycelial plugs, fragments of actively growing mycelium from agar cultures, as an inoculum source (see Table 1.2). This is typical when exploring effects on woody tissues, and was used to perform Koch's postulates on *Lithocarpus densiflorus* and *Quercus agrifolia* in saplings and mature trees in California (Rizzo et al. 2002).

The other typical inoculum source is an aqueous zoospore suspension (Parke et al. 2002, Moralejo and Hernandez 2002). Less frequently, other forms of diaspore suspension have been used: sporangia (de Gruyter et al. 2002), and sporocysts (Delatour et al. 2002). Dosage is more easily attenuated by dilution and plants do not require wounding. Also, zoospores are known to be infective propagules, thus inoculation simulates natural infection better than mycelial plug.

In the present study, detached leaf assays are used to test the susceptibility of a large number of native species not widely propagated, including rare species. Plant species that were available as whole plants were inoculated using similar techniques: a zoospore suspension of adequate concentration for producing consistent symptoms on naturally infected hosts.

Table 1.2 Matrix of plant tissues and inoculum sources for bioassays with *Phytophthora ramorum* (not exhaustive)

	Leaves	Logs	Stems	Whole plants
Mycelial plugs	Inman et al. 2002 Linderman et al. 2002	Hansen et al. 2002 Brasier et al. 2002	Werres et al. 2001+ Hansen et al. 2002 Rizzo et al. 2002+ Tooley and Kyde 2003	Delatour et al. 2002 Rizzo et al. 2002+ Tooley and Englander 2002
Zoospore suspension	Hansen et al. 2002 Inman et al. 2002 Moralejo and Hernandez 2002 Parke et al. 2002			Parke et al. 2002. Delatour et al. 2002 (sporocysts)

+ = used for Koch's postulates

Chapter 2. Potential susceptibility of tanoak associated vegetation to *Phytophthora ramorum* in southwestern Oregon

2.1 Abstract

Phytophthora ramorum infects many hosts besides oaks, and the prognosis is that more plant species will become hosts as the range of the pathogen expands. Tanoak (*Lithocarpus densiflorus*) is the principal suscept in California and southwestern Oregon, and is abundant in many plant associations. Using detached leaf and whole plant assays, tanoak-associated species not known to be hosts for *P. ramorum* were exposed to the pathogen in the laboratory and growth chamber. These were compared with known hosts to ascertain the potential for susceptibility in the field. Questions are raised about the likelihood for infection of certain species based on habitat.

2.2 Introduction

Sudden oak death (SOD), caused by *Phytophthora ramorum*, has killed tens of thousands of oak and tanoak trees in coastal northern and central California (Rizzo et al. 2002). The disease has spread rapidly, spanning over 600 km of the west coast of the United States since first observed in California around 1994 (Davidson et al. 2003).

In August 2001, the Oregon Department of Agriculture, working in conjunction with the Oregon Department of Forestry, Oregon State University, and the USDA Forest Service, announced that *P. ramorum* had been isolated from symptomatic tanoaks in forests near Brookings, Oregon, at the extreme southwestern corner of the state (Goheen et al. 2002).

The discovery of the pathogen, and finding that the initial infestations were clustered within a nine-square mile (23.3 km^2) area and represented a total of approximately 16 ha, prompted an effort to attempt eradication by cutting and destroying infected individuals and surrounding individuals of known host species, burning the plant material, and broadcast burning a 15-30 m buffer area (Goheen et al. 2002b).

In addition to tanoak (*Lithocarpus densiflorus* [Hook. & Arn.] Rehd. var. *densiflorus*), and true oaks of the black oak subsection (*Quercus*, subsect. Erythrobalanus), *P. ramorum* has been isolated on selective media and detected by molecular methods (PCR) on many other hosts, and was originally described from ornamental rhododendrons and viburnum in European nurseries (Werres et al. 2001). The breadth of the plant taxa affected, and the rate of discovery of new hosts, suggests that many more new plant species may be affected by the pathogen (Rizzo et al. 2002b). While few are affected to the degree that inspired the common name of the disease caused by this pathogen, many other taxa may be killed or experience branch dieback or foliar blight (Rizzo et al. 2002b, Hansen et al. 2002, Garbelotto et al. 2003) with uncertain effects on important plant processes (Davidson et al. 2003). These other hosts play an important role in the pathosystem. *Umbellularia californica* (Lauraceae: Oregon myrtlewood/ California bay laurel) may not be severely impacted by infection, but generates large amounts of inoculum that is shed into the forest, infecting other species. In Oregon however, *P. ramorum* has seldom been recovered from *U. californica* (Goheen et al. 2002c). New hosts have been encountered in Oregon, and many taxa that are hosts in California have yet to be affected by the disease in Oregon.

Thus, the screening of species associated with tanoak in Oregon contributes to a defensive approach to battling the pest. Many of these species are not propagated commercially, thus we employ a detached leaf assay to test these species, and whole plant assays to screen species for which cultivated plants are available. The efficacy of detached leaf assays in determining whole plant response has been assessed for *P. infestans*, causal in potato late blight (Dorrance and Inglis 1997). Also, many others have used detached leaf assays and whole plant assays to investigate potential host status for *P. ramorum* (Hansen et al. 2002, Inman et al. 2002, Linderman et al. 2002, Moralejo and Hernandez 2002, Parke et al. 2002), which have proven to have predictive value in the case of *Arbutus unedo* (Moralejo, in press), and cultivars of *Viburnum* (Inman et al. 2003).

2.3 Methods and Materials

2.3.1 Tanoak associations

USDA Forest Service ecologists have characterized the forests of southwestern Oregon and northwestern California by defining association types and the most abundant species present therein (Atzet et al. 1996, Jimerson et al. 1996). In this study, we've focused principally on broadleaf tree, shrub and herb species, as others have been examining the effects of *P. ramorum* on conifers (Hansen et al. 2002, Denman et al. 2003, G. Chastagner, personal communication). Leaves of each species (~100 g/species, from 2 or more individuals/site) were collected from 10 sites within the Siskiyou National Forest (Chetco, Galice, Gold Beach, and Illinois Valley Ranger Districts) under permit between July 2002 and July 2003. A list of the most common tanoak associated species is provided in Appendix A.

2.3.2 *Phytophthora ramorum* isolation and culture

Isolates of *Phytophthora ramorum* were collected from infected tanoak, evergreen huckleberry, and Pacific rhododendron by E. M. Hansen, J.L. Parke, and W. Sutton. Initial isolations were on corn meal agar amended with 200 mg L^{-1} ampicillin, 10 mg L^{-1} rifampicin, and 20 mg L^{-1} pimaricin (CARP), which were transferred onto ~1/3 strength clarified V8 agar to foster rapid axenic growth and zoosporangia production. Isolates were maintained at room temperature (~20 °C) until sporangial harvest.

Sporangia were harvested by flooding 2-3 week old petri dish cultures with 2 aliquots of 5 mL sterile water (autoclaved reverse osmosis filtered water), gently sweeping with a rubber policeman to dislodge the aerial sporangia. Batches (30 mL) were chilled at 4 °C for 1 hour, and incubated at room temperature for 1 hour to stimulate zoospore release. The resulting suspension was filtered through a 35-µm nylon mesh to remove sporangia, chlamydospores and hyphae. The zoospores were counted with a hemacytometer, and the suspension diluted to the desired concentration (6×10^4 zoospores mL^{-1} for detached leaf assays, 3×10^4 zoospores mL^{-1} for whole plant inoculations).

2.3.3 Zoospore efficacy

To test the infective potential of zoospores, zoospore suspension (described above) was filtered (5 µm Millipore filter), and leaves of *Vaccinium ovatum* (a known host) dipped petiole down in the resultant filtrate, unfiltered zoospore suspension, and sterile water. Aliquots of each suspension (1 mL) were plated on CARP to determine the presence of live pathogen.

2.3.4 Dose Response

Leaves of *Vaccinium ovatum* were dipped halfway, petiole down in a zoospore suspension at rates of 10^5, 10^4, 10^3, 10^2 zoospores mL^{-1} and sterile water as a negative control. Consistent infection developed only in the 10^5 zoospore mL^{-1} treatment.

2.3.5 Detached Leaf Assay

Assays were performed on ten separate dates between July 2002 and July 2003. Different subsets of the species were tested on each date, such that each species was tested on two separate dates from two different sites. On each trial date, 10 leaves of each species were dipped halfway, petiole down, in either sterile water or a zoospore suspension (6×10^4 zoospores mL^{-1}) for approximately five seconds, and incubated in a moist chamber at room (~20 °C) temperature for 7 days. The moist chamber was a plastic box (30 cm × 21 cm × 9 cm) with a tight fitting lid lined with paper towels moistened with sterile water. Dipped leaves were placed on the paper towels, in a manner to avoid contact between leaves, covered with a plastic frame, and more moist paper towels placed on top of the frame before sealing the boxes.

At harvest the leaves were digitally photographed, and symptomatic lesions plated on CARP to reisolate the pathogen. All species were assayed twice or more, and in each assay a known host was included as a positive control (typically *Vaccinium ovatum* or *Lithocarpus densiflorus*).

2.3.5 Whole Plant Assay

Seedlings and young plants of a subset of Oregon tanoak associates were obtained from the Oregon Department of Forestry. For each species, the aerial portion of ten plants was dipped in zoospore suspension (3.0×10^4 zoospores mL^{-1}), or in sterile water as a negative control. Each plant was dipped for approximately five seconds.

After inoculation, plants were covered with plastic bags propped with bamboo stakes to maintain humidity and to reduce the possibility of pathogen escape and contamination of water-inoculated plants. Plants were incubated in a growth chamber for 3 weeks.

At harvest, leaves were removed from each plant and digitally photographed. After photographing, pieces of symptomatic lesions on leaves and stems were plated on CARP to reisolate the pathogen.

2.3.6 Image Analysis

Leaves were photographed digitally on a blue felt background with a Nikon Coolpix or Canon PowerShot S110 Digital Elph, and percent lesion area determined using APS Assess (Landari 2002). Photographs were enhanced by selecting 'autocontrast' to improve sensitivity of the image analysis software.

Table 2.1 Tanoak associated species inoculated with *Phytophthora ramorum* in detached leaf and whole plant dip assays

			Detached Leaf Assay			Whole Plant Assay		
Species	Common name	Family	Date#	Incidence	% Necrosis(SD)	% Incidence (SD)	n	% Lesion Area (SD)
Alnus rubra	Red alder	Betulaceae	3, 8	5/5, 5/5	7.9(5.6), 2.1(3.3)			
Berberis nervosa	Dwarf Oregon-grape	Berberidaceae	1, 2	5/5, 5/5	0.6(0.1), 0.7(0.4)	26.2 (10.5)	5	9.1 (11.1)
Chimaphila umbellata	Prince's pine	Ericaceae	1, 2, 4	4/5, 5/5	18.4(30.6), 33.6 (19.9)			
Chrysolepis chrysophylla	Western chinquapin	Fagaceae	1, 2, 4	5/5, 4/5, 5/5	25.9(21.4), 8.1(3.5), 1.3(0.8)			
Cornus nuttallii	Western dogwood	Cornaceae	9, 10	5/5, 5/5	92.6(8.1), 95.2(6.3)			
Gaultheria shallon	Salal	Ericaceae	2, 6	1/5, 3/5,	0.2(0.5), 3.9(4.8)	70.82 (16.65)	5	18.0 (13.0)
Linnaea borealis	Western twinflower	Caprifoliaceae	1, 2	5/5, 5/5	100(0), 82.3(41.8)			
*Lithocarpus densiflorus**	Tanoak	Fagaceae	1, 3, 4	5/5, 5/5, 5/5	46.3(12.5), 10.1(4.3), 1.8(0.5)	91.5 (14.4)	5	23.8 (21.0)
Pinus lambertiana	Sugar pine	Pinaceae	1, 3	0/5, 0/5	0(0), 0(0)			
Pinus monticola	Western white pine	Pinaceae	1, 3	0/5, 0/5	0(0), 0(0)			
Pinus ponderosa	Ponderosa pine	Pinaceae	1,3	0/5, 0/5	0(0), 0(0)			
Polystichum munitum	Western swordfern	Dryopteridaceae	2, 6, 7	0/5, 0/5, 0/5	0(0), 0(0)			
Pteridium aquilinum	Brackenfern	Dennstaedtiaceae	3, 7	0/5, 0/5	0(0), 0(0)			
*Quercus chrysolepis***	Canyon live oak	Fagaceae				86.1 (8.2)	5	13.4 (8.0)
*Quercus kelloggii***	California black oak	Fagaceae	4	5/5	16.8 (7.0)			
Quercus sadleriana	Sadler oak	Fagaceae	1, 2	5/5, 5/5	32.7(28.3), 1.1(0.5)	60.2 (14.6)	5	10.2 (7.1)
Quercus vaccinifolia	Huckleberry oak	Fagaceae	1, 3	5/5, 5/5	13.2(23.0), 2.0(1.1)	71.6 (21.9)	5	16.0 (16.0)

* = natural host for *P. ramorum* in California and Oregon, ** = at present, natural host for *P. ramorum* in California only.

Table 2.1 Tanoak associated species inoculated with *Phytophthora ramorum* in detached leaf and whole plant dip assays (continued)

			Detached Leaf Assay			Whole Plant Assay		
Species	Common name	Family	Date#	Incidence	% Necrosis (SD)	% Incidence (SD)	N	% Lesion Area (SD)
*Vaccinium ovatum**	Evergreen huckleberry	Ericaceae	4, 5, 6, 9, 10	5/5, 4/5, 5/5, 10/10, 5/5	24.0 (19.1), 36.7(27.1), 28.6 (12.6), 4.3(3.3), 68.7 (40.1)	85.8 (12.0)	5	79.7 (13.3)
Vaccinium parvifolium	Red huckleberry	Ericaceae	1, 2, 4, 5	4/5, 4/4, 5/5, 5/5	80.0(44.7), 50.4 (55.7), 52.3(47.5), 87.0 (16.7)			
Whipplea modesta	Western modesty	Hydrangeaceae	9, 10	5/5, 5/5	46.0 (22.4), 36.9 (16.9)			
Xerophyllum tenax	Beargrass	Liliaceae	3, 8	0/5, 0/5	0 (0), 0 (0)			

* = natural host for *P. ramorum* in California and Oregon, ** = at present, natural host for *P. ramorum* in California only.

Date#: 1= July 18, 2002; 2= July 23, 2002; 3= August 2, 2002; 4= September 2, 2002; 5= September 5, 2002; 6= October13, 2002; 7= February 11, 2003; 8= May 08, 2003; 9= May 23, 2003; 10= June 23, 2003.

Incidence: For each assay date, incidence is the number of leaves with lesions/number of leaves treated
% Necrosis (SD): For each trial date, the average % necrotic area for all treated leaves and the standard deviation.

% Incidence (SD): for the whole plant assay, the average percentage of leaves that developed lesions caused by *P. ramorum* and the standard deviation.
% Lesion Area (SD): Of the leaves that were incident, the average lesion area and standard deviation.

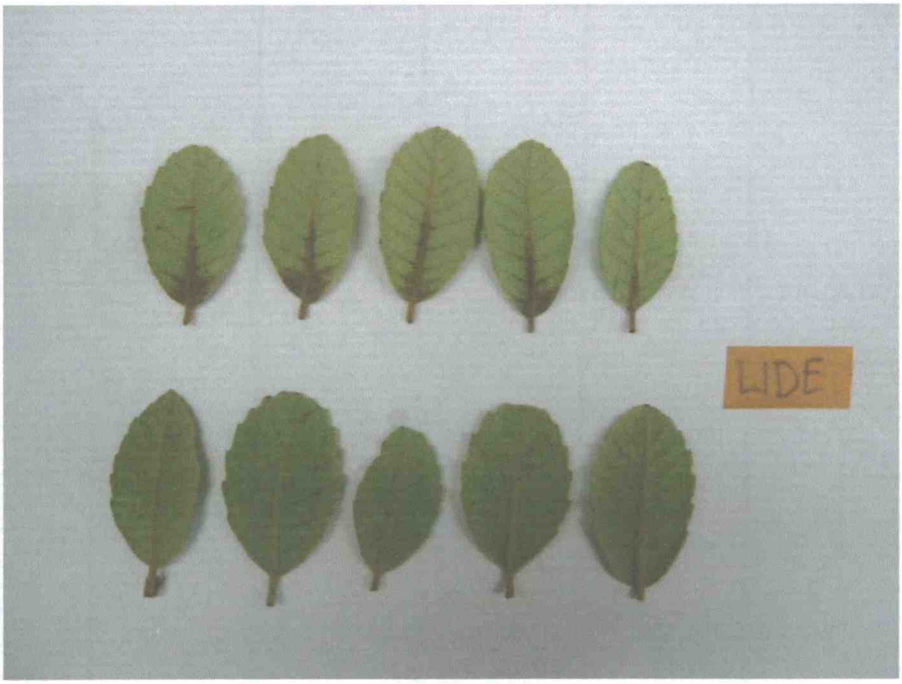


Figure 2.1 Abaxial view of leaves of tanoak (*Lithocarpus densiflorus*) inoculated with *Phytophthora ramorum* (above) and uninoculated sterile water control (below). Orange tape is 3 cm long.

Figure 2.2 Abaxial view of leaves of Sadler oak (*Quercus sadleriana*, subsection Quercus) inoculated with *Phytophthora ramorum* (above) and sterile water control (below). White tape is ~5 cm long.

Figure 2.3 Adaxial view of leaves of chinquapin (*Chrysolepis chrysophylla*) inoculated with *Phytophthora ramorum* (left) and sterile water control. Leaves are ~8 cm long.

Figure 2.4 Adaxial view of leaves of red huckleberry (*Vaccinium parvifolium*) inoculated with *Phytophthora ramorum* (above) and sterile water control (below). Ruler = 10 cm.

Figure 2.5 Adaxial view of leaves of twinflower (*Linnaea borealis*) inoculated with *Phytophthora ramorum* (above) and sterile water control (below). Leaves are approximately 1.5 cm long.

Figure 2.6 Abaxial view of leaflets of western swordfern (*Polystichum munitum*) inoculated with *Phytophthora ramorum* (above) and sterile water control (below). Ruler = 10 cm.

2.3.7 Analysis of disease

2.3.7.1 Detached leaf assays

Inoculated and control leaves were incubated in the same moist chamber, and control leaves were occasionally contaminated. This was confirmed by plating on CARP, and the results from those leaves discarded. Also, since leaves were not surface sterilized prior to inoculation, symptoms of infection by opportunistic microbes were occasionally observed, and the results discarded when noninoculated leaves became symptomatic.

2.3.7.2 Whole plant assays

For each species and treatment, the following data were collected at harvest: total number of leaves on each plant, average lesion area for all leaves, number of incident leaves, and percent incidence (incident leaves/total number of leaves).

In all detached leaf and whole plant assays, plant materials were autoclaved after harvest and containers sterilized with 10% sodium hypochlorite (Clorox) solution.

2.4 Results

2.4.1 Detached leaf assays

Most of the tanoak-associated species tested developed lesions when exposed to zoospores of *Phytophthora ramorum* (see Table 2.1) in detached leaf assays (13/21 = 62%). In all assayed species of the oak family, necrosis appeared to be predominantly in the midrib and vascular tissue. In other assayed susceptible species, dark lesions developed throughout the dipped portion of the leaf blade, though occasionally spot lesions, apparently from single zoospore infections, were evident. All species in which lesions developed were significantly greater than controls ($p < 0.05$) (Figures 2.1-2.4). Percent lesion area was highly variable between species and treatment dates/sites (Table 2.1). This variability was observed in all of the known hosts, and rarely affected incidence, which was consistent for most species.

The two species of fern, three species of pine, and monocot (*X. tenax*) did not develop lesions when exposed to *P. ramorum* (see Figure 2.5). Although several coniferous species have been reported as natural and experimental hosts, members of the genus *Pinus* appear to be less susceptible or resistant (Denman et al. 2003, Hansen et al. 2002, K. Riley, personal communication). To date, no monocots or pteridophytes have been reported as hosts from the field or laboratory inoculations.

Zoospore-free filtrate did not induce symptoms on the known host *Vaccinium ovatum*, suggesting that live zoospores are necessary for infection.

2.4.2 Whole plant assays

All seven species developed lesions caused by *P. ramorum* in whole plant assays and the pathogen was recovered from lesions in leaves and stems.

The health of some control plants declined over the course of the experiment that may have been due to cultural conditions. Leaves of many of the Sadler oak seedlings had a scorched appearance at the margins before the initiation of the experiment. Symptoms caused by *P. ramorum* were evident, though the severity of the infestation may have been exacerbated by condition of the plants prior to inoculation.

In some plant species, lesions were very small. *Berberis nervosa* appeared to have limited symptoms in both detached leaf and whole plant assays. Incidence was high and severity low in both experiments, suggesting this species may be a less susceptible, though not resistant, host for *P. ramorum*.

In salal (*Gaultheria shallon*), incidence and severity were both low in detached leaf assays, but symptoms were frequent and severity high in whole plant inoculations. Phenology may have played an important role in this result. The inoculated whole plants were young, with copious succulent new growth, and the detached leaves were from established, field-collected plants. Others have found younger leaves to be more susceptible than older leaves (J.L. Parke, unpublished).

Tanoak and canyon live oak, when inoculated with isolates of *P. ramorum*, developed lesions in foliage and on stems, which served as a template for observing the other oaks in the whole plant experiment. In all oak taxa tested, lesions developed along the midribs of infected leaves, extending into the petiole and stem. This includes a member of the white oak subsection (subsection Lepidobalanus, *Q. sadleriana*), which has not been observed to be symptomatic in California.

Foliar symptoms were similarly found at the base of the leaf in detached leaf and whole plant assays. Additionally, cankers developed in the stems though none of the plants had been killed at harvest, and some had new growth at the base. The pathogen was recovered from leaves and stems of all of the treated whole plants, and none of the uninoculated controls, on selective media (CARP).

2.5 Discussion

An understanding of the host range of a pathogen is essential knowledge for any study of the epidemiology, transmission, and control of that pathogen. In California, many plant species are known to be hosts for *Phytophthora ramorum*, while in Oregon, few species have been found naturally infected. The extent that this is due to the geographic range of the pathogen in each state, or due to climatic or other factors, is unknown. The former case (range) is highly likely, and given current knowledge the latter (other factors) may be true, at least for *U. californica*. The climatologic optima and range for *P. ramorum* are not yet known, nor is the role that weather plays in transmission. In Oregon's nine-square-mile quarantine area three different tanoak association types (as defined by Atzet et al. 1996) are found near the infestations. These associations are the highest mean annual temperature and precipitation for the tanoak series. However, these sites are spatially clustered, thus the possibility of spread into other association types merits investigation. Presently, risk models typically focus primarily on climatic conditions, or on potential hosts in a broad taxonomic sense (i.e. "oaks" or "red oaks"). By looking at potential hosts more specifically, the acuity of these models may be enhanced.

Our goal in performing these assays is to determine which species commonly found in associations with tanoak may also be susceptible to *Phytophthora ramorum*. The design of these experiments is such that the conditions are permissive for the growth of the pathogen, rather than approximating the typical field conditions under which one might find the taxa being assayed. We have evaluated physiological susceptibility; the putative host is exposed to the pathogen, but in an artificial environment.

Environmental factors are important in disease development *in situ*, and certainly species that develop the greatest lesion severity are not necessarily at greatest risk. *Gaultheria ovatum*, apparently highly susceptible, is typically found at high elevation sites. *Gaultheria shallon*, which detached leaf data suggests is less susceptible than *G. ovatum*, is frequently found in more mesic sites at a wide range of elevation. *G. shallon* is certainly at greater risk of being challenged by the pathogen.

Susceptibility of fagaceous species is important to understanding risk to plant communities in southwestern Oregon. All of the oak species (including tanoak) developed very similar lesions in detached leaf and whole plant assays. Canyon live oak (*Quercus chrysolepis*), included in the whole plant assay, is a naturally infected host in California, although only from a single site. It is the first reported oak host not of the red/black oak subsection (Erythrobalanus) and widely distributed throughout California and southwestern Oregon; it is of the intermediate oak subsection (Protobalanus) (Murphy and Rizzo 2002). Huckleberry oak is closely related to canyon live oak (hybrids exist), and is typically found at elevations over 900 m in the Siskiyous and in the Sierra Nevadas although it may be found at lower elevations and closer to the Pacific Ocean on serpentine (Atzet et al. 1996). Sadler oak (*Q. sadleriana*) is an endemic shrub typically found over 600 m elevation, and is of the white oak subsection (Lepidobalanus). No white oaks have yet been infected with *P. ramorum* in California. Chinquapin (*Chrysolepis chrysophylla*) is a widely distributed species in southwestern Oregon, and may be found in the coastally influenced association types such as those where *P. ramorum* has been found. It is closely related to tanoak (Manos et al. 2001), and previous study suggests that it may develop the "sudden oak death" disease type based on log inoculations (Hansen et al. 2002). Our leaf inoculations, although unable to differentiate between disease types, support this result, though in the case of the shrubby true oaks, the difference between sudden oak death and ramorum dieback may be subtle.

Gaultheria shallon and *Berberis nervosa* are two of the most abundant understory species in western Oregon. Our results suggest that *B. nervosa* is susceptible to the pathogen though severity of symptoms was consistently low in detached leaf and whole plant assays. In detached leaf assays, incidence and severity were both low for *G. shallon*. In whole plant assays, incidence and severity were high, which may be due to the abundance of actively growing succulent tissue, which other assays have shown to be more susceptible than mature tissue.

Lack of susceptibility in vitro is also an important result, as it counters the argument that any vascular plant species can be a host for *P. ramorum* if inoculum density is adequately high. In a small subset of species, symptoms were not observed in any of the treated leaves. The two species of ferns assayed, *Polystichum munitum* and *Pteridium aquilinum*, are also abundant throughout western Oregon and beyond. Beargrass (*Xerophyllum tenax*) is also common, and is found in the infested area near infected tanoak. In this case, field evidence supports our finding of resistance *in vitro*.

Phytophthora ramorum may alter community composition by affecting plant species in two general ways: disease in individuals of a susceptible species may alter community composition directly by killing or hindering members of that species (autecological effects), and susceptible species, which may or may not be damaged by the pathogen may serve as sources of inoculum for other susceptible species (synecological effects). The present study does not indicate which disease types are most likely to occur in each of the experimental hosts, nor species' relative contributions to inoculum production. However, this study does suggest that the pathogen would not be host limited if it establishes in Oregon.

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Chapter 3. Potential for *Phytophthora ramorum* to infect rare ericaceous species of the Siskiyou Mountains, southwestern Oregon

3.1 Abstract

Phytophthora ramorum, causal agent in sudden oak death, affects many species in the Ericaceae. The pathogen has been introduced into southwestern Oregon, and eradication efforts have sought to eliminate the pathogen. The nearby Siskiyou Mountains harbor many endemic species, some of conservation concern. We assayed three ericaceous species of conservation concern for susceptibility to *P. ramorum* using a detached leaf assay; *Arctostaphylos hispidula*, *Kalmiopsis leachiana*, and *Leucothoe davisiae* and several associated species. While all three rare species developed spreading foliar lesions when exposed to the pathogen, habitat and other factors will determine whether the pathogen will threaten these experimental hosts.

3.2 Introduction

Oaks, although the most severely impacted hosts of the sudden oak death pathogen *Phytophthora ramorum*, are not the principal hosts (Rizzo et al. 2002, Garbelotto et al. 2003). The taxonomic range of hosts is broad and plant families such as the Ericaceae (heath family) are disproportionately affected (Rizzo et al. 2002b). The number of host taxa within this family has increased with the expansion of the oomycete's geographic range (see Table 3.1). Thus, the introduction of *P. ramorum* in southwestern Oregon (Goheen et al. 2002) constitutes a threat not only to tanoak

Table 3.1 Ericaceous hosts for *Phytophthora ramorum*.

Host	Common name/varieties	Typical symptoms	Mortality?	Location	Mating type	Source
Arbutus menziesii	Pacific madrone		Yes (small plants)	California	A2	Rizzo et al. 2002b
A. unedo	Strawberry tree		Unknown	Spain	A1	Moralejo, in press
Arctostaphylos manzanita	Manzanita	Leaf blight	Unknown	California	A2	Rizzo et al. 2002b
Kalmia latifolia	Moutain laurel	Leaf blight	Unknown	UK	A1	COMTF 2003
Pieris spp.	Andromeda	Leaf blight,	Unknown	Europe (UK), Oregon (nursery)	A1	Inman et al. 2003, Osterbauer et al. 2003
Rhododendron spp.	Ornamental rhododendron (many cultivars)	Dieback	Yes	California, Europe, Oregon, Washington state, British Columbia	A1 and A2	Werres et al. 2001
Rhododendron macrophyllum	Pacific rhododendron	Dieback, leaf blight	Yes	California, Oregon (forest)	A2	Goheen et al. 2002
Vaccinium ovatum	Evergreen huckleberry	Dieback	Yes	California, Oregon	A2	Rizzo et al. 2002, Goheen et al. 2002

(*Lithocarpus densiflorus*) and California black oak (*Quercus kelloggii*), both hosts in California, but to other taxa including many not yet exposed to the pathogen in nature.

The Klamath Mountains of northwestern California and southwestern Oregon are recognized for their great richness in vascular plant species (Whittaker 1960, Stebbins and Major 1966) and harbor many endemic species (Smith and Sawyer 1988). The Siskiyou Mountains, which straddle the western Oregon/California border, are the northernmost of the Klamath Ranges, extending from the Rogue River in the north to the Klamath River in the south, and inland from near the Pacific Ocean to the junction with the Cascade Mountains east of Ashland, OR.

With the discovery of *Phytophthora ramorum* in southwestern Oregon (Goheen et al. 2002), and subsequent eradication efforts (Goheen et al. 2002b), natural resource managers have adopted an active and focused approach to disease management. We wanted to determine if Siskiyou native plant species, including those of conservation concern, are also susceptible to this pathogen.

The Oregon Natural Heritage Program (ONHP) maintains databases of rare animal and plant populations in concert with governmental agencies to assist in the process of monitoring these taxa for potential listing by act of federal, state and local endangered species legislation (ONHP 2001). It is from this list that the three rare ericaceous species were selected for testing, based and geographic location. Because the number of host species is steadily increasing, we also tested the susceptibility of species associated with these rare taxa to gain some preliminary information regarding effects of the pathogen at the community level.

3.2.1 *Arctostaphylos hispidula*

Arctostaphylos hispidula is Oregon's only rare manzanita (ONHP 2001). Known commonly as Gasquet manzanita or hairy manzanita, it is most abundant in the Smith River National Recreation Area (formerly Gasquet Ranger District) on the Six Rivers National Forest in California, with several populations in the adjacent Siskiyou National Forest in Oregon. Two disjunct populations are known from northern Sonoma County, California (Bouldin 1992, CalFlora 2000). Otherwise the species is found only in the western Siskiyous (ONHP 2001). It is often found on serpentine, and infrequently on sandstone (Wells 2000).

The species is monitored by several agencies, including ONHP, the California Native Plant Society (CNPS), the USDA Forest Service (USFS), and USDI Bureau of Land Management (BLM). ONHP places *A. hispidula* on list 2: "species which are threatened, endangered, or possibly extirpated from Oregon, but are stable or more common elsewhere" (ONHP 2001). CNPS uses a similar system for determining priority of rare species (Skinner and Pavlik 1994). *A. hispidula* is on CNPS' list 4 (the "watch" list, plants of limited distribution), as the species is more abundant in adjoining Del Norte County, CA.

The genus *Arctostaphylos* has been problematic for the pathologists studying *P. ramorum*. *A. manzanita* is on the host list in California, discovered by molecular techniques (PCR), though a culture has yet to be obtained from live host material (Davidson et al. 2003). It is not known whether the pathogen causes mortality on this host, though the closely related *Arbutus menziesii* (madrone) may be killed by *P. ramorum* (Davidson et al. 2003). Artificially inoculated manzanita develops lesions comparable in size with other ericaceous hosts (Rizzo et al. 2002b). It is one of the least understood native hosts for *P. ramorum* (D.M. Rizzo, personal communication). *A. uva-ursi*, (kinnikinnick) the only circumboreal species (Wells 2000), also develops disease symptoms when artificially inoculated with the pathogen (Tooley and Englander 2002). In these species, as many other ericaceous species, stem dieback develops.

3.2.2 *Kalmiopsis leachiana*

This genus is endemic to southwestern Oregon, with the majority of occurrences in the Kalmiopsis Wilderness within the Siskiyou National Forest and managed by the USFS. A disjunct metapopulation exists in the North Umpqua River watershed, approximately 200 km northwest of the Siskiyous in the Cascade Mountains. Oregon botanists consider it a distinct species, *Kalmiopsis fragrans* Kaye and Meinke (in prep); based on several characteristics such as its substrate preference, flower morphology, and fragrance (T.N. Kaye, personal communication). The North Umpqua kalmiopsis has been horticulturally propagated with limited success, but not so the Siskiyou species.

ONHP ranks the Siskiyou species, *Kalmiopsis leachiana*, as G4S4 and places it on list 4, meaning the plant is not imminently threatened or endangered (though possibly rare) (ONHP 2001). The North Umpqua metapopulation is much smaller than that of the Siskiyous and is on ONHP's list 1, with global and state rankings of 1, meaning the plant species is critically imperiled due to rarity, and fewer than 5 occurrences are known. *K. fragrans* is also a "Species of Concern", meaning the US Fish and Wildlife Service (USFWS) is reviewing the species for potential listing under the federal Endangered Species Act (ONHP 2001).

In both species, the plant is a low evergreen shrub with deep rose, campanulate flowers bearing golden glands on the abaxial surface of the leaves (Peck 1961). Marquis (1978), who studied the ecology and distribution of *Kalmiopsis*, described three general habitat types for the plant: two in the Siskiyous (high and low altitude) and one in the Cascades (before the North Umpqua populations were treated as a separate species). The majority of populations are at altitudes greater than 900 m, though a substantial number are found at lower altitude, between 400-600 m. While *K. leachiana* may be found on serpentine, it is not a serpentine endemic (Marquis 1978, Love 1991).

3.2.3 *Leucothoe davisiae*

Leucothoe davisiae is on the ONHP's list 3, meaning it is rare in Oregon though more common elsewhere (ONHP 2001), in this case the Sierra Nevada in California (CalFlora 2000). At a recent conference reviewing the status of rare species in Oregon, it was suggested by USFS and BLM staff that the species be upgraded to list 2 (ONHP 2003) (as is *A. hispidula*). CNPS does not consider *L. davisiae* a plant species of conservation concern.

The plant is an erect shrub typically less than 1.5 m, with oblong-elliptic leaves up to 6 cm long. It is found in areas with wet soils from 1300-2600 m from the Klamath Ranges south to the Warner Mountains and Sierra Nevada (Peck 1961, Hickman 1993). In Oregon, it has been described from only one association type, with Port-Orford-cedar (*Chamaecyparis lawsoniana*) at the highest elevations of its range in the Siskiyous (Zobel et al. 1985, Atzet et al. 1996).

Members of the genus of 8 recognized species (Mabberley 1997) are often used as ornamentals. Species are native to the Himalayas and Japan (Mabberley 1997) as well as the United States, where 5 species are found (USDA, NCRS 2002). *L. davisiae* (Sierra-laurel) is the only native species found in the western United States (USDA, NCRS 2002). Ornamental leucothoe is susceptible to *P. ramorum* in detached leaf assays comparing the pathogen to other commonly encountered *Phytophthora* species (Linderman et al. 2002), and in an English nursery, ornamental *Leucothoe fontanesiana* cv. Rainbow has been found to be naturally infected with *P. ramorum* (A. Inman, personal communication).

3.2.4 Rationale for the study

Many factors contribute to the rarity of plant species, though introduced pathogens have not been widely considered. The most well studied exception is *Phytophthora cinnamomi*, an oomycete with a host range on the order of a thousand species, introduced into many habitats worldwide but most notably Australia (Zentmyer 1980). The number of plant taxa infected by *P. cinnamomi* in Australia has been unparalleled; 75% of the plant species may be killed on a site (Weste and Marks 1987), and rare taxa are not exceptions (Barker 1994, Peters and Weste 1997).

In this study we test these three rare ericaceous species and common associated species for susceptibility to *P. ramorum* in detached leaf assays. This protocol has been used to assess whole plant response of potato to *P. infestans* with some success (Dorrance and Inglis 1997). Other researchers studying *P. ramorum* have used similar methods to investigate the potential host range of the pathogen in horticulturally important taxa

(Inman et al. 2002, Linderman et al. 2002, Moralejo and Hernandez 2002, Parke et al. 2002), and cases exist where artificially inoculated hosts have subsequently been found infected naturally. Detached leaf assays only require a small sacrifice of host leaves, which minimizes impact on the species being assayed. The habitats of these species are considered to inform hypotheses addressing risk to these species.

3.3 Methods and Materials

3.3.1 Rare plant selection

Rare species for this study were selected from the ONHP list of rare plants; Membership in the Ericaceae, presence in the Klamath Ranges, and presence in Josephine and Curry Counties were the search criteria. Locations of populations of the three plant species identified were furnished by ONHP, USFS, and the Oregon State University Herbarium (OSC). Leaves were collected from two or more individuals of each of the rare species and associated taxa at each site (100 g total for each species) on each collection date. A list of plant species commonly associated with each species is provided in Appendix B.

All species were collected by permission from USFS, from the locations and on the dates listed in table 3.2. The leaves were kept on ice until use in the detached leaf assay, typically within 12-48 hours of harvest.

3.3.2 *Phytophthora ramorum* handling

Phytophthora ramorum was isolated from infected tanoak, evergreen huckleberry, and Pacific rhododendron by E. M. Hansen, J.L. Parke, and W. Sutton. Initial isolations were on corn meal agar amended with 200 mg L^{-1} ampicillin, 10 mg L^{-1} rifampicin, and 20 mg L^{-1} pimaricin (CARP), which were transferred onto ~1/3-strength clarified V8 agar to foster rapid growth and sporangia production. Isolates were maintained at room temperature (~20 °C) until sporangia harvest.

Sporangia were harvested by flooding each 2-3 week old petri dish culture with 2 aliquots of 5 mL sterile water (autoclaved reverse osmosis filtered water), and gently sweeping with a rubber policeman to dislodge the sporangia. Batches of 30 mL were chilled at 4 °C for 1 hour, and incubated at room temperature for 1 hour to stimulate zoospore release. The resulting suspension was filtered through a 35-µm nylon mesh to remove sporangia, chlamydospores and hyphae. The zoospores were counted with a hemacytometer, and the suspension diluted to a concentration suitable for producing consistent symptoms on a known host (*Vaccinium ovatum* [see previous chapter]).

3.3.3 Detached leaf assay

At each trial 10 leaves of each species were dipped halfway, petiole down, in either sterile water or a zoospore suspension (6×10^4 zoospores mL^{-1}) for approximately five seconds. Dipped leaves were incubated in a moist chamber at room temperature for 7 days (~20 °C). The moist chamber was a plastic box (30 cm × 21 cm × 9 cm) with a tight fitting lid lined with paper towels moistened with sterile water. Dipped leaves were

Table 3.2: Locations from which rare plants and associated species were collected

Species	General Location	Township Range and Section*	Date	Notes
Arctostaphylos hispidula	Mount Emily	T40S R12W S7	6 July 2002	
	Palmer Butte	T40 R13 S10	2 February 2003	< 2 km from SOD quarantine area
Kalmiopsis leachiana	Salamander Lake	T38S R11W S26	21 May 2003	Collected after Biscuit Fire 2002
	Gardner Mine	T39S R11W S3	21 May 2003	Collected after Biscuit Fire
Leucothoe davisiae	Flat Top	T36S R9W S20	5 July 2002	Collected before Biscuit Fire 2002
	Bunker Hill Mine	T35S R9W S2	18 June 2003	Collected by T.N. Kaye et al.

*Precise locations of rare species are available from the author upon request placed on the paper towels in a manner to avoid contact between leaves, covered with a plastic frame, and more moist paper towels placed on top of the frame before sealing the boxes.

At harvest the leaves were digitally photographed, and symptomatic lesions plated on CARP to reisolate the pathogen. All species were assayed twice or more, and in each assay a known host was included as a positive control (typically *Vaccinium ovatum* or *Lithocarpus densiflorus*).

To address the question of whether the point of detachment constitutes a wound that would provide an artificial infection court, a subset of leaves of *K. leachiana* and *L. davisiae* were dipped petiole down or petiole up, and percentage lesion area compared using a two-sample t-test.

3.3.4 Image analysis

Leaves were photographed digitally on a blue felt background with a Nikon Coolpix or Canon PowerShot S110 Digital Elph, and percent lesion area determined using APS Assess (Landari 2002). Photographs were enhanced by selecting the 'autocontrast' feature, which improved sensitivity.

3.3.5 Analysis of disease

Inoculated and control leaves were incubated in the same moist chamber, and control leaves were occasionally contaminated. This was confirmed by plating on CARP, and the results from these leaves discarded. Also, since leaves were not surface sterilized prior to inoculation, opportunistic microbes were occasionally observed, and the results discarded when noninoculated leaves became symptomatic.

In all assays, plant materials were autoclaved after harvest to destroy the pathogen, and the moist chambers washed in 10% bleach (sodium hypochlorite) solution.

3.4 Results

Leaves of all three of the rare plants developed symptoms similar to known *P. ramorum* hosts when challenged with the pathogen (Figure 3.1-3.3), as did many of their associates not previously challenged with the pathogen (22/28 = ~78%). The severity of the symptoms, or the percentage of leaf area that became necrotic, differed within species between separate assay dates, but the incidence, or number of leaves developing symptoms in each trial, was consistent for most species (Table 3.3-Table 3.4). In all cases except species that were resistant, lesion area of treated leaves were significantly greater than control leaves ($p << 0.05$).

Most of the ericaceous species developed dark necrotic lesions that advanced past the inoculation front, showing that the pathogen had spread through uninoculated tissue. In associated species of the Fagaceae (beech family), the midrib and vascular tissue became necrotic. In species in other families necrosis advanced throughout the leaf blade, similar to the ericaceous species. Occasionally spot lesions developed, suggesting that the pathogen had established on the leaf surface originating from a single propagule.

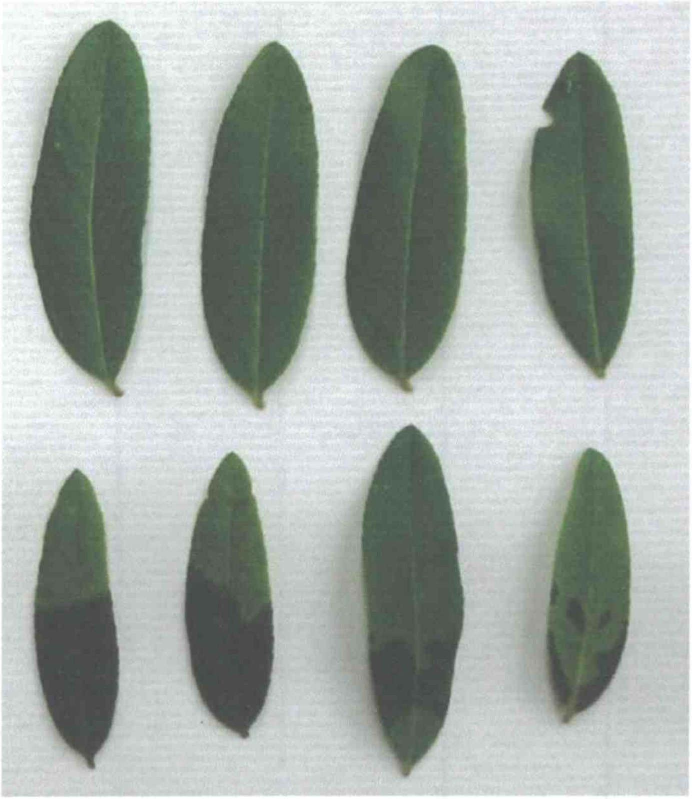

Figure 3.1 Adaxial view of leaves of sierra-laurel (*Leucothoe davisiae*) inoculated with *Phytophthora ramorum* (below) and sterile water control (above). Leaves are ~ 6-8 cm long.

Figure 3.2 Abaxial view of leaves of *Kalmiopsis leachiana* inoculated with *Phytophthora ramorum* (above) and sterile water control (below)

Figure 3.3 Leaves of Gasquet manzanita (*Arctostaphylos hispidula*) inoculated with *Phytophthora ramorum* (below) and sterile water control (above). Leaves are ~1.5-2.5 cm.

Table 3.3 Species associated with rare ericaceous plants, tested for susceptibility to *Phytophthora ramorum* in detached leaf assays.

Species	Common name	Family	Species associate#			% Incidence	N	% Severity (sd)
			ARHI	KALE	LEDA			
Arctostaphylos columbiana	Hairy manzanita	Ericaceae	+			100	10	97.3 (4.5)
Arctostaphylos hispidula	Gasquet manzanita	Ericaceae	+			100	10	50.9 (46.4)
Arctostaphylos nevadensis	Pinemat manzanita	Ericaceae	+	+		90	10	84.6 (32.0)
Ceanothus velutinus	Tobaccobrush	Rhamnaceae	+			40	10	1.9 (4.0)
Garrya buxifolia	Boxleaf silktassel	Garryaceae	+			87	15	12.9 (11.3)
Gaultheria ovatifolia	Wintergreen	Ericaceae			+	100	9	90.0 (16.3)
Holodiscus discolor	Oceanspray	Rosaceae	+			100	10	31.6 (17.5)
Kalmiopsis leachiana	Kalmiopsis	Ericaceae		+	+	100	40	27.4 (18.1)
Leucothoe davisiae	Sierra-laurel	Ericaceae		+	+	80	20	19.7 (21.1)

ARHI = *A. hispidula*, KALE = *K. leachiana*, and LEDA = *L. davisiae*

Table 3.3 Species associated with rare ericaceous plants, tested for susceptibility to *Phytophthora ramorum* in detached leaf assays (continued).

Species	Common name	Family	Species associate#			% Incidence	N	% Severity (sd)
			ARHI	KALE	LEDA			
*Rhamnus californica***	California coffeeberry	Rhamnaceae	+	+		100	10	2.9 (6.1)
Rhododendron occidentale	Western azalea	Ericaceae	+		+	57	14	4.5 (5.6)
Vaccinium scoparium	Grouse whortleberry	Ericaceae			+	100	15	42.3 (16.7)

ARHI = *A. hispidula*, KALE = *K. leachiana*, and LEDA = *L. davisiae*, ** *R. californica* is a natural host for *P. ramorum* in California

Table 3.4 Rare plant associated species inoculated with *Phytophthora ramorum* in detached leaf assays.

Species	Common name	Family	Associated with#			Detached Leaf Assay		
			ARHI	KALE	LEDA	% Incidence	N	Mean % lesion area (SD)
Alnus rubra	Red alder	Betulaceae			+	90	10	5.0 (5.4)
Berberis nervosa	Dwarf Oregon-grape	Berberidaceae	+	+	+	100	10	0.7 (0.3)
Chimaphila umbellata	Prince's pine	Ericaceae	+	+	+	93	15	50.7 (41.5)
Chrysolepis chrysophylla	Western chinquapin	Fagaceae	+	+	+	90	10	11.8 (15.7)
Cornus nuttallii	Western dogwood	Cornaceae	+	+		90	10	94.1 (6.9)
Gaultheria shallon	Salal	Ericaceae	+	+	+	40	10	2.1 (3.8)
Linnaea borealis	Western twinflower	Caprifoliaceae		+	+	100	10	90.7 (29.6)
*Lithocarpus densiflorus**	Tanoak	Fagaceae	+	+	+	100	15	19.7 (21.1)
Pinus lambertiana	Sugar pine	Pinaceae		+	+	0	10	0 (0)
Pinus monticola	Western white pine	Pinaceae	+	+	+	0	10	0 (0)
Pinus ponderosa	Ponderosa pine	Pinaceae	+	+	+	0	10	0 (0)
Polystichum munitum	Western swordfern	Dryopteridaceae		+	+	0	15	0 (0)
Pteridium aquilinum	Brackenfern	Dennstaedtiaceae		+	+	0	10	0 (0)
*Quercus kelloggii***	California black oak	Fagaceae			+	100	5	16.8 (7.0)
Quercus sadleriana	Sadler oak	Fagaceae	+	+	+	100	10	16.9 (25.2)
Quercus vaccinifolia	Huckleberry oak	Fagaceae	+	+		100	10	7.6 (16.4)
*Vaccinium ovatum**	Evergreen huckleberry	Ericaceae	+	+		97	30	29.1 (32.6)
Vaccinium parvifolium	Red huckleberry	Ericaceae	+	+	+	95	20	68.4 (12.0)
Whipplea modesta	Western modesty	Hydrangeaceae	+	+	+	100	5	46.0 (22.4)
Xerophyllum tenax	Beargrass	Liliaceae	+	+	+	0	10	0 (0)

* = natural host for *P. ramorum* in California and Oregon, ** = at present, natural host for *P. ramorum* in California only. # ARHI = *A. hispidula*, KALE = *K. leachiana*, and LEDA = *L. davisiae*

In the assay, petiole direction did not significantly affect the percentage of lesion area on either *K. leachiana* ($p = 0.33$, 18 df) or *L. davisiae* ($p = 0.82$, 8 df), and thus wounding did not appear to influence the results.

A high amount of variability was observed in the severity (percent lesion area) data within species between treatment dates/sites, including known hosts. Incidence (number of leaves developing lesions) was more consistent in the majority of species.

3.5 Discussion

As the number of host species and geographic range of *P. ramorum* increase, a question remains as to which species are likely to be challenged by the pathogen in the future, and what the impact upon those species may be.

The infestation in Oregon presently suggests a narrow range of climatic optima for *P. ramorum*, though this may be due to the size of the area where the pathogen has been recovered from infected individuals, < 40 acres (16 ha) total within nine-square miles (23.3 km^2). In order for disease to manifest outside of this area, appropriate environmental factors must accompany the meeting of host and pathogen.

Populations of *Arctostaphylos hispidula* are found within 2 km of the quarantine area. Thus physical proximity puts this species at greatest risk of the three rare taxa. Most populations are found in the western Siskiyous and within 80 km of the coast, though typically on serpentine soils in an open canopy shrub community. While these last two factors may mitigate the risk of *P. ramorum* infecting *A. hispidula* given current knowledge of the pathogen's biology, several known hosts are common associates, including: *Lithocarpus densiflorus, Rhododendron macrophyllum,* *Umbellularia californica* and *Vaccinium ovatum*, and many other experimental hosts reported here including other species of manzanita.

A. hispidula is Oregon's only rare manzanita (ONHP 2001). California, by contrast, has 60 rare taxa including subspecies and varieties, including 33 in infested counties (Skinner and Pavlik 1994). Many of these are locally adapted in the extreme, being found on a single substrate type or on a single geographic feature (Wells 2000). Thus, many of California's rare manzanitas may also be at risk.

Kalmiopsis leachiana is also associated with the principle known hosts and several experimental hosts. Like *A. hispidula*, it may be found at altitude over 900 m, though populations are found down to 300 m elevation, and it may be found in closed canopy forests.

With rare exception, *Kalmiopsis leachiana* sensu stricto is found within the Kalmiopsis Wilderness, an area managed by the USFS and intended to be "an area which is affected primarily by the forces of nature" (Anonymous, 1998). Thus, if *P. ramorum* is found on *K. leachiana* under natural conditions, a conundrum arises whereby the limitation of management options may adversely affect the eponymous plant the area is intended to protect. Populations of the other two rare species are found within the Wilderness, though they are not similarly restricted to the Wilderness.

Phytophthora lateralis, also introduced into southwestern Oregon, is present in the Kalmiopsis Wilderness. Visitors to the area are warned of the dangers of spreading *P. lateralis*, which infects Port-Orford cedar (*Chamaecyparis lawsoniana*) (Figure 3.4). Similar signage may help reduce spread of *P. ramorum* in the wilderness, although much remains unknown about transmission of the SOD pathogen.

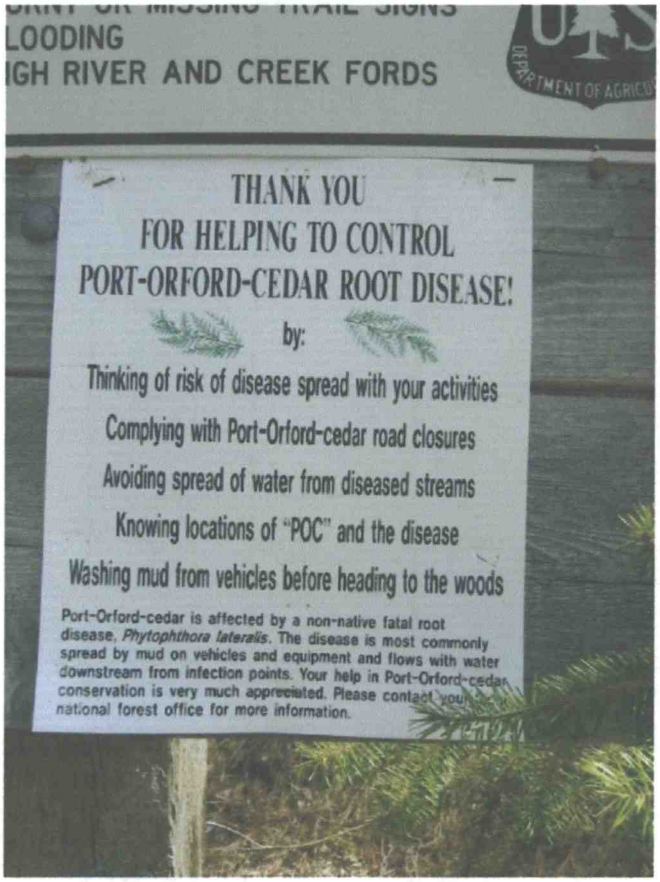

Figure 3.4 Sign informing visitors to the Kalmiopsis Wilderness about *Phytophthora lateralis*

Leucothoe davisiae is found at the highest elevation of the three species, and with one exception, all known populations are further inland than the other rare species. *Rhododendron macrophyllum* is a common associate, but *Lithocarpus densiflorus* and *U. californica* are rarely observed. Again, many species associated with sierra-laurel also appear to be susceptible in detached leaf assays.

Sudden oak death has become the well-known common name for the disease caused by *Phytophthora ramorum*, but several other species are affected, and not all succumb to the infection. Pathogens need not be lethal in order to effect change on individuals, populations, and communities. Individuals that develop foliar blight do not only lose a portion of their photosynthetic production, which would have effects on growth and fitness; other physiological disruption may occur, which increases the penalty of infection and may affect other important processes including reproduction and thus fitness.

The distribution of *Phytophthora ramorum* in native forests of western North America suggests an exotic origin, and the breadth of hosts infected further complicates prediction of community impacts. Reduction of species richness may be expected, as has been seen in Australian sites affected by *P. cinnamomi*, and similarly rare taxa may be threatened with extinction or extirpation.

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Chapter 4. Conclusion

Phytophthora ramorum, causal in sudden oak death and related diseases, is likely to infect many broadleaf species of the western Siskiyou Mountains not previously recognized as hosts. The novelty of the introduction and the novelty of the species to science make predicting effects on plant communities difficult. Further complicating the task is the breadth of host taxa and variety of disease types.

Two approaches to prioritizing species for testing have been pursued. The first was to examine species associated with the principal tree host in Oregon, *Lithocarpus densiflorus*. Tanoak's central role in sudden oak death in Oregon, coupled with the increasing number of naturally infected plant taxa, justifies this approach to identifying potential hosts for *Phytophthora ramorum*. The second approach was to identify species that possess value. In this study, ericaceous Siskiyou plants of conservation concern are the "target" species.

Diseases in native ecosystems and, more dramatically, diseases caused by exotic pathogens may affect their habitats at several levels simultaneously. Change may occur at the landscape, community, species, population, individual, and genetic levels.

Tanoak community structure may be altered by directly reducing numbers of individuals of species that are susceptible, as well as increasing the amount of inoculum in a community. Chapter 2 considers the potential changes in landscape and community that may accompany a large infestation by *P. ramorum*.

Chapter 3 considers rare species in southwestern Oregon, which are not currently imperiled although the pathogen may negatively affect the species in the long term. The reason these species were selected was due to concern about the effects of the pathogen on the level of species, which means effects on populations, individuals and genes.

For the rare plants, habitat conditions may be the most important factors in mitigating the risk of infection. While moisture and temperature certainly are important variables determining the range of the pathogen, the extremes tolerated by *P. ramorum* in the field are not known. Many of the site characteristics that direct the distribution of plant species will affect the distribution of the pathogen. These include but are not limited to: elevation, annual precipitation, soils (e.g. serpentine), temperature extremes, canopy cover (*P. ramorum* has been found mostly in closed canopy forests) and management.

In the near future, two datasets will be made public that will greatly enhance the potential for host based modeling using the data presented in this thesis. The USDA-Forest Service is creating a digital map of the forested associations in southwestern Oregon. In the field guide, average percent cover and constancy for each species are given, as well as average annual precipitation and average annual temperature. Having maps of association groups can therefore generate a climate and host based risk map for the area including the data presented in this thesis.

Also, the Oregon Flora Project is creating an online digital atlas of Oregon's plant taxa, with locality data for every specimen in the Oregon State University Herbarium as well as from species lists compiled by botanists. The data gathered here can be used with these two databases to create a geographic information system (GIS) model of disease risk in all of Oregon's natural communities.

Eradication efforts in Oregon, to date, have reduced the spread of *Phytophthora ramorum*, though the oomycete is still present. An understanding of the hosts that may become infected is an important part of preventing the infestation from becoming established, or managing the pathogen if eradication becomes impracticable.

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APPENDICES

APPENDIX A. List of major tanoak associated species

Conifer species associated with tanoak in the Siskiyou Mountains (species data from Atzet et al. 1996, Jimerson et al. 1996).

Species	Common name	Family	Pr host status	Source	Habitat notes
Calocedrus decurrens	Incense-cedar	Cupressaceae	Unknown		
Chamaecyparis lawsoniana	Port-Orford-cedar	Cupressaceae	No, but principal host for *P. lateralis*		
Pinus attenuata	Knobcone pine	Pinaceae	Unknown		
Pinus jeffreyi	Jeffrey pine	Pinaceae	Unknown		
Pinus lambertiana	Sugar pine	Pinaceae		In this thesis	
Pinus monticola	Western white pine	Pinaceae		In this thesis	
Pseudotsuga menziesii	Douglas-fir	Pinaceae	Yes, apparently at high inoculum pressure	Davidson et al. 2002b	Abundant, present in most areas
Tsuga heterophylla	Western hemlock	Pinaceae		Denman et al. 2003	Coastal, low elevation, moist areas
Taxus brevifolia	Pacific yew	Pinaceae	In UK, *T. baccata*	COMTF 2003	

Broad-leafed tree and shrub species associated with tanoak in the Siskiyou Mountains (species data from Atzet et al. 1996, Jimerson et al. 1996).

Species	Common name	Family	Pr host status	Source	Habitat notes
Acer circinatum	Vine maple	Aceraceae			Cool, often riparian
Acer macrophyllum	Bigleaf maple	Aceraceae	Yes, in CA	Rizzo et al. 2002b	
Alnus rubra	Red alder	Betulaceae		In this thesis	Wet, streamside, low elevation, coastal
Arbutus menziesii	Madrone	Ericaceae	Yes, in CA	Rizzo et al. 2002b	
Arctostaphylos spp.	Manzanita	Ericaceae	*A. manzanita* in CA, PCR only	Rizzo et al. 2002b	
			A. uva-ursi in whole plant assays	Tooley and Englander 2002	
			Other *Arctostaphylos* spp.	In this thesis	
Chrysolepis chrysophylla	Chinquapin	Fagaceae		In this thesis	
Cornus nuttallii	Western dogwood	Cornaceae		In this thesis	
Corylus cornuta var. *californica*	Hazelnut	Betulaceae	Yes, in California	Rizzo et al. 2002b	
Quercus chrysolepis	Canyon live oak	Fagaceae	Yes, in CA	Murphy and Rizzo 2002	Most widely distributed oak sp. in CA

Species	Common name	Family	Pr host status	Source	Habitat notes
Quercus garryana	Oregon white oak	Fagaceae	Not in field, limited symptoms in laboratory inoculations	Rizzo et al. 2002b	
Quercus kelloggii	California black oak	Fagaceae	Yes, in CA	Garbelotto et al. 2001	Warm, inland, middle elevation
Quercus sadleriana	Sadler oak	Fagaceae		In this thesis	Open stands, high elevation, cool, moist sites near Pacific Ocean Siskiyou endemic
Quercus vaccinifolia	Huckleberry oak	Fagaceae		In this thesis	High elevation, often on serpentine, low tree cover Siskiyou endemic
Rhododendron macrophyllum	Pacific rhododendron	Ericaceae	Yes, CA and OR	Rizzo et al. 2002b; Goheen et al. 2002	mid elevation, cool, close to Pacific Ocean, moist
Rhododendron occidentale	Western azalea	Ericaceae		In this thesis	Cool, wet, acidic soils
Umbellularia californica	Oregon myrtlewood/bay-laurel	Lauraceae	Yes, very important in CA, not very important in OR	Garbelotto et al. 2003, Goheen et al. 2002d	Moist, low elevation,
Vaccinium ovatum	Evergreen huckleberry	Ericaceae	Yes, in California and Oregon	Goheen et al. 2002, Rizzo et al. 2002, in this thesis	Moist, low elevation, coastal or foggy sites
Vaccinium parvifolium	Red huckleberry	Ericaceae		In this thesis	Cool, high elevation, often on serpentine

Understory species associated with tanoak in the Siskiyou Mountains (species data from Atzet et al. 1996, Jimerson et al. 1996).

Species	Common name	Family	Pr host status	Source	Habitat notes
Berberis nervosa	Dwarf Oregon-grape	Berberidaceae		In this thesis	Cool, steep, high elevation, moderate shrub cover
Chimaphila menziesii		Ericaceae	Unknown		
Chimaphila umbellatum	Prince's pine	Ericaceae		In this thesis	
Gaultheria shallon	Salal	Ericaceae	Only from PCR (Rizzo, pers. comm.)	In this thesis	Mid-elevation sites with high shrub cover
Linnaea borealis	Twinflower	Caprifoliaceae		In this thesis	
Lonicera hispidula	Honeysuckle	Caprifoliaceae	Yes, in CA	Rizzo et al. 2002	Low elevation, interior
Polystichum munitum	Western swordfern			In this thesis	
Pteridium aquilinum	Brackenfern			In this thesis	
Rosa gymnocarpa		Rosaceae			
Toxicodendron diversilobum	Poison-oak	Anacardiaceae	Yes, in OR and CA	Goheen et al. 2002c, COMTF 2002	
Trientalis latifolia	Western starflower	Primulaceae	Yes, in CA	Hüberli et al. 2002	
Whipplea modesta	Western modesty	Hydrangeaceae		In this thesis	

APPENDIX B. List of plant species commonly associated with rare Ericaceous taxa of the Siskiyou Mountains.

Common Associates of *Arctostaphylos hispidula.*

Conifers

Species	Common name	Family	Source	Pr host status
Chamaecyparis lawsoniana	Port-Orford-cedar	Cupressaceae	O	
Pinus attenuata	Knobcone pine	Pinaceae	B, Za	
Pinus monticola	Western white pine	Pinaceae	B	-
Pinus ponderosa	Ponderosa pine	Pinaceae	B	-
Pinus jeffreyi	Jeffrey pine	Pinaceae	B, O	
Pseudotsuga menziesii	Douglas-fir	Pinaceae	B, O, Za	*

Broadleaf trees and shrubs

Species	Common name	Family	Source	Pr host status
Arbutus menziesii	Madrone	Ericaceae	B	*
Arctostaphylos columbiana	Hairy manzanita	Ericaceae	B, Za	+
Arctostaphylos nevadensis	Pinemat manzanita	Ericaceae	B, Za	+
Arctostaphylos patula	Greenleaf manzanita	Ericaceae	O	+
Arctostaphylos viscida	Sticky manzanita	Ericaceae	O	
Ceanothus cuneatus	Whitetop buckthorn	Rhamnaceae	O	
Ceanothus velutinus	Tobaccobrush	Rhamnaceae	O	+
Chrysolepis chrysophylla	Tall chinkapin	Ericaceae	O, Za	+
Corylus cornuta var. *californica*	Hazelnut	Betulaceae	O	*
Garrya spp.	Silktassel	Garryaceae	O, Za	+
Holodiscus discolor	Oceanspray	Rosaceae	O	+
Lithocarpus densiflorus	Tanoak	Fagaceae	O, Za	**
Quercus chrysolepis	Canyon live oak	Ericaceae	O, Za	*

Common Associates of *Arctostaphylos hispidula* (continued)

Broadleaf trees and shrubs

Species	Common name	Family	Source	Pr host status
Quercus sadleriana	Sadler oak	Fagaceae	O	+
Quercus vaccinifolia	Huckleberry oak	Fagaceae	O, Za	+
Rhamnus californica	California coffeeberry	Rhamnaceae	O, Za	*
Rhododendron macrophyllum	Pacific rhododendron	Ericaceae	O, Za	**
Rhododendron occidentale	Western azalea	Ericaceae	O	+
Rhus diversilobum	Poison-oak	Anacardiaceae	O	**
Rosa spp.	Rose	Rosaceae	O	
Rosa gymnocarpa	Baldhip rose	Rosaceae	O	
Rubus spp.	Blackberry	Rosaceae	O	
Umbellularia californica	Oregon myrtlewood/bay-laurel	Lauraceae	O	*
Vaccinium parvifolium	Red huckleberry	Ericaceae	O, Za	+
Vaccinium ovatum	Evergreen huckleberry	Ericaceae	O, Za	**

Herbs

Species	Common name	Family	Source	Pr host status
Berberis nervosa	Dwarf Oregon-grape	Berberidaceae	O	+
Chimaphila umbellata	Prince's pine	Ericaceae	O	+
Epilobium minutum	Small willowweed	Onagraceae	O	
Eriophyllum lanatum	Oregon sunshine	Asteraceae	O	
Goodyera oblongifolia	Rattlesnake plantain	Orchidaceae	O	
Lonicera hispidula	Hairy honeysuckle	Caprifoliaceae	O, Za	*
Whipplea modesta	Western modesty	Hydrangeaceae	O	+
Xerophyllum tenax	Beargrass	Liliaceae	O, Za	-

B= Bouldin 1992, O= Oregon Natural Heritage Project tracking data 2002, Za = data collected by the author 2002-2003
Key: * = known *Phytophthora ramorum* (Pr) host in California, ** = known Pr host in Oregon and California, + = tested in this thesis and susceptible, - = tested in this thesis and resistant

Common Associates of *Kalmiopsis leachiana*

Conifers

Species	Common name	Family	Source	Pr host status
Chamaecyparis lawsoniana	Port-Orford-cedar	Cupressaceae	M, Za	
Picea breweri	Brewer spruce	Pinaceae	M	
Pinus attenuata	Knobcone pine	Pinaceae	M	
Pinus lambertiana	Sugar pine	Pinaceae	Za	-
Pinus monticola	Western white pine	Pinaceae	M	-
Pseudotsuga menziesii	Douglas-fir	Pinaceae	M, Za	*

Broadleaf trees and shrubs

Species	Common name	Family	Source	Pr host status
Arbutus menziesii	Madrone	Ericaceae	M	*
Arctostaphylos canescens	Manzanita	Ericaceae	M	
Arctostaphylos nevadensis	Pinemat manzanita	Ericaceae	M	+
Ceanothus pumilus		Rhamnaceae	M, Za	
Chrysolepis chrysophylla	Chinkapin	Fagaceae	Za	+
Cornus nuttallii	Western dogwood	Cornaceae	M	+
Garrya fremontii	Bearbrush	Garryaceae	M, Za	
Gaultheria shallon	Salal	Ericaceae	M, Za	+
Lithocarpus densiflorus	Tanoak	Fagaceae	M, Za	**
L. densiflorus var. echinoides	Dwarf tanoak	Fagaceae	M, Za	?
Quercus chrysolepis	Canyon live oak	Fagaceae	M, Za	*
Quercus vaccinifolia	Huckleberry oak	Fagaceae	M, Za	+
Rhamnus californica	California coffeeberry	Rhamnaceae	M	*
Rhododendron macrophyllum	Pacific rhododendron	Ericaceae	M, Za	**
Rhus diversilobum	Poison-oak	Anacardiaceae	M	**
Rosa gymnocarpa	Baldhip rose	Rosaceae	M	
Rubus ursinus	Pacific blackberry	Rosaceae	M	

Common Associates of *Kalmiopsis leachiana* (continued)

Broadleaf trees and shrubs

Species	Common name	Family	Source	Pr host status
Symphoricarpus albus	Snowberry	Caprifoliaceae	M	+
Umbellularia californica	Oregon myrtlewood /bay-laurel	Lauraceae	M, Za	*
Vaccinium ovatum	Evergreen huckleberry	Ericaceae	M, Za	**
Vaccinium parvifolium	Red huckleberry	Ericaceae	M, Za	+

Herbs

Species	Common name	Family	Source	Pr host status
Achlys triphylla	Vanilla leaf	Berberidaceae	M	
Arnica parviflora		Asteraceae	M	
Berberis nervosa	Dwarf Oregon-grape	Berberidaceae	M	+
Berberis pumilus		Berberidaceae	M	
Chimaphila umbellatum	Prince's pine	Ericaceae	M	+
Linnaea borealis	Twinflower	Caprifoliaceae	M	+
Lonicera hispidula	Hairy honeysuckle	Caprifoliaceae	M	*
Whipplea modesta	Western modesty	Hydrangeaceae	M	+
Xerophyllum tenax	Beargrass	Liliaceae	M, Za	-

M=Marquis 1978, Za= collected by the author 2003.
Key: * = known *Phytophthora ramorum* (Pr) host in California, ** = known Pr host in Oregon and California, + = tested in this thesis and susceptible, - = tested in this thesis and resistant

Common Associates of *Leucothoe davisiae*

Conifers

Species	Common name	Family	Source	Pr host status
Abies concolor	White fir	Pinaceae	O, Zo	
Chamaecyparis lawsoniana	Port-Orford-cedar	Cupressaceae	O, Zo	
Pinus lambertiana	Sugar pine	Pinaceae	O, Za	-
Pinus monticola	Western white pine	Pinaceae	O, Za	-
Pinus ponderosa	Ponderosa pine	Pinaceae	Za	-
Pseudotsuga menziesii	Douglas-fir	Pinaceae	O, Za, Zo	*
Taxus brevifolia	Western yew	Taxaceae	A	
Tsuga heterophylla	Western hemlock	Pinaceae	O, Zo	

Broadleaf trees and shrubs

Species	Common name	Family	Source	Pr host status
Alnus rubra	Red alder	Betulaceae	O, Za	+
Chrysolepis chrysophylla	Tall chinkapin	Fagaceae	O, Za	+
Gaultheria shallon	Salal	Ericaceae	A, O, Za	+
Quercus garryana	Oregon white oak	Fagaceae	O	
Quercus sadleriana	Sadler oak	Fagaceae	A, Za	+
Rhododendron macrophyllum	Pacific rhododendron	Ericaceae	A, O, Za	*
Rhododendron occidentale	Western azalea	Ericaceae	Za	+
Rubus ursinus	Blackberry	Rosaceae	A, O	
Vaccinium parvifolium	Red huckleberry	Ericaceae	A, Za,	+

Common Associates of *Leucothoe davisiae* (continued)

Herbs

Species	Common name	Family	Source	Pr host status
Asarum caudatum	Wild ginger	Aristolochiaceae	O	
Berberis nervosa	Dwarf Oregon-grape	Berberidaceae	A, O	+
Blechnum spicant	Deer fern	Blechnaceae	O	
Chimaphila menziesii	Small prince's pine	Ericaceae	A, Za	
Gaultheria ovatifolia	Wintergreen	Ericaceae	Za	+
Goodyera oblongifolia	Rattlesnake plantain	Orchidaceae	A	
Linnaea borealis	Twinflower	Caprifoliaceae	A, Za	+
Polystichum munitum	Western swordfern	Dryopteridaceae	A, Za	-
Pteridium aquilinum	Brackenfern	Dennstaedtiaceae	A, Za	-
Trillium ovatum	Wake-robin	Liliaceae	A	
Vaccinium scoparium	Grouse whortleberry	Ericaceae	Za	+
Whipplea modesta	Western modesty	Hydrangeaceae	O, Za	+
Xerophyllum tenax	Beargrass	Liliaceae	A, O, Za	-

A=Atzet et al. 1996, I= data collected by Institute for Applied Ecology 2003, O=Oregon Natural Heritage Program tracking data 2002, Za=data collected by the author 2002-2003, Zo=Zobel et al. 1985

Key: * = known *Phytophthora ramorum* (Pr) host in California, ** = known Pr host in Oregon and California, + = tested in this thesis and susceptible, - = tested in this thesis and resistant