# INTRODUCED FOREST PATHOGENS: PORT-ORFORD-CEDAR ROOT DISEASE

BY

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A THESIS

Presented to the Environmental Studies Program
and the Honors College of the University of Oregon
in partial fulfillment of the requirements
for the degree of
Bachelor of Arts

September 2004

APPROVED: [redacted]

An Abstract of the Thesis of

Katherine Weidman for the degree of Bachelor of Arts

In the Environmental Studies Program to be taken September 2004

Title: INTRODUCED FOREST PATHOGENS: PORT-ORFORD-CEDAR ROOT DISEASE

Approved: [redacted]

An exotic fungal forest pathogen, *Phytophthora lateralis,* first identified in the Pacific Northwest in 1923, eventually spread throughout much of the Port-Orford-cedar tree's native range, killing significant amounts of this valuable timber species on high-risk sites. In 1997, the United States Forest Service started a Port-Orford-cedar breeding program to increase resistant varieties of this tree to be replanted in areas of its native range. Beginning on a species level, and expanding to a broader geographical and ecosystem-based context, this paper describes ecological and biological differences between Port-Orford-cedar and other similar species within a forest, as well as the effects of different forest pathogens. What are the characteristics and impacts of native, versus introduced, forest pathogens on forests within the range of Port-Orford-cedar? Should there be a human responsibility towards protecting native species, such as the Port-Orford-cedar, from pathogens that we have introduced? If so, what should that responsibility be?

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# INTRODUCTION

The exotic fungal forest pathogen *Phytophthora lateralis* appeared in the Pacific Northwest in the early twentieth-century, eventually spreading throughout much of the Port-Orford-cedar's native range, and destroying a portion of one of the most valuable timber species in southwestern Oregon. In 1997, the United States Forest Service, in cooperation with other federal agencies, private landowners, tribes, and other organizations, began a Port-Orford-cedar breeding program with the hope of breeding resistant varieties to be replanted in areas of the tree's native range. The story of this pathogen, the extent to which humans were involved in spreading it throughout watersheds, and the effort to stop it illustrates some of the changes humans have brought about in the northwest forests over the last two hundred years. This thesis is written for myself and my peers—both science majors and liberal arts students—in hopes that it will educate people about the issue, and inspire a curiosity to learn more. This paper will look at the science, ecology, and ethics of either losing significant portions of a tree species or altering them for resistance to human-introduced pathogens, focusing on the Port-Orford-cedar root disease.

Understanding the relationship between this exotic pathogen and the Port-Orford-cedar tree involves not only knowledge of fungal and forest biology, but also an understanding of the geology, geography, and watersheds of the regions. Indirectly, the subject is related to the nursery trade, controversies over old-growth forests and logging roads, responsibilities towards human-introduced species, the economy of the Pacific Northwest, and aesthetic values that people attribute to this tree, its wood, and its wood products.

## I. History and Background of the Disease

The Port-Orford-cedar tree, *Chamaecyparis lawsoniana* (figure 1), is one of the most beautiful, elegant, and highly valued of Pacific Northwest timber species. Port-Orford-cedar's native range is from southwest Oregon, southward into northwest California (figure 2). It is especially common near Coos Bay and Port Orford, Oregon. It ranges in elevation from sea level up to around 5,000 feet (Jensen, Randall, Keniston and Beaver 2002). Port-Orford-cedar does not grow naturally anywhere else in the world, although it has been widely planted as an ornamental tree. Port-Orford-cedars prefer very wet, cool locations along streams and swamps, where water is abundant throughout the summer. They grow slower than most conifers, growing well both as colonizers[1], in direct sunlight, and as understory trees in highly shaded areas. Growing around 125-200 feet tall and three to six feet in diameter[2], they are the largest species of the *Chamaecyparis* genus (Jensen et al 2002; Final Supplemental Environmental Impact Statement [FSEIS] 2004). They are important to watersheds for their close association with streams, since they can grow with their roots submerged in water. They also grow well on ultramafic soils,[3] where many other canopy species grow poorly. Because their wood is highly rot resistant and will remain in streams for a very long time, they are important in creating pools and riffles for salmon and other aquatic species. Older trees have very thick, fire-resistant bark and produce abundant seed crops (figure 3), while

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[1] Colonizer species are often the first species to regenerate on disturbed sites, such as cleared or burned areas.

[2] The largest Port-Orford-cedar in the world, growing in the Powers Ranger BLM District, is almost 12 feet in diameter (FSEIS 2004).

[3] Ultramafic soils contain high amounts of heavy metals such as iron and magnesium.

their seedlings regenerate quickly following disturbance, making them a successful species in fire-prone ecosystems.

Considered by many to have the most valuable wood in the world, Port-Orford-cedar is prized for the strength and beauty of its wood, its straight-splitting grain, its resistance to rot, and its pleasant "gingery" odor. Its wood is highly prized by the Japanese, whose woodworkers use it as a replacement for one of their vanishing native, highly valued species, *Chamaecyparis obtusa*, the Hinoki cypress. Port-Orford-cedar plays a historically important role in the culture, traditions, and medicinal practices of many Native Americans who live within its range. They use its straight-grained wood for buildings and sweat-lodges, as well as for arrows and lances. Its bark and roots have been used for mats, clothing, baskets, twine, and other items (Final Supplemental Environmental Impact Statement [FSEIS] 2004). Its boughs are also appreciated in the floral industry (figure 3), where they are preserved and dyed various colors, and used as wreaths and garlands. It has also been widely cultivated in nurseries to be used as an ornamental tree. Before root disease became a problem, it was cultivated into more than two hundred varieties, leading to its planting as a landscape species in many locations outside of its range.

The root disease causing fungus, *Phytophthora lateralis,* is known to cause widespread mortality only in *Chamaecyparis lawsoniana*, Port-Orford-cedar. It also affects and sometimes kills Pacific yew, *Taxus brevifolia*, although only when it is found growing in close association with diseased Port-Orford-cedar. Symptoms of the "fungal disease" caused by *Phytophthora lateralis* were first reported in 1923, in Port-Orford-cedar seedlings being grown for the ornamental trade in a nursery near Seattle, Washington. This was well outside of the native range of Port-Orford-cedar. It killed, within a few years of introduction, nearly 90% of the trees it came into contact with. At that time, biologists recognized the devastating impact the fungus would have on the species if it spread. The pathogen proceeded to spread southward, mainly via ornamentally planted species. Dying Port-Orford-cedars were seen in the Willamette Valley by 1937. Within 19 years of this first report, the pathogen reached the native range of Port-Orford-cedar, in Southwestern Oregon. In the three years following its introduction, the pathogen became established along the coast and up into the more highly populated river valleys of Curry and Coos Counties (Zobel, Roth and Hawk 1985).

Spores of *Phytophthora lateralis* spread through water and in mud, as well as from the roots of infested trees to their neighbors. In the earlier part of this century, the disease spread quickly throughout watersheds, ridge-tops, and along logging roads, where the spores were carried mainly by human activity. Logging trucks and the heavy machinery related to logging picked up and carried a great deal of mud, serving as the primary vectors for the fungus. In a study done in Southern Oregon and California in 2002, the pathogen was present in all major watersheds in the study-area. Furthermore, most—26 of 36 locations, or 72%—of the separate infection sites coincided with locations where creeks are crossed by roads (Jules, Kauffman, Ritts and Carroll 2002). Of the 65 creeks in this study, only 10 % of those without roads crossing them were infected with the pathogen—and all of these infections were downhill from a road (Jules et al. 2002). Near the more southern extent of its range, where Port-Orford-cedar occur primarily along streams, the entire lengths of infected streams will generally become infested and contain many dead, standing Port-Orford-cedar within a decade of initial signs of the pathogen (Jules et al. 2002).

Although the origin of *Phytophthora lateralis* is unknown, it is suspected to come from somewhere outside of the native range of Port-Orford-cedar, because of the sudden and devastating effect on the species. Also, given that the first observation of *Phytophthora lateralis* was outside of the native range of Port-Orford-cedar, and that it was involved in a nursery trade where plants were being shipped between the United States and Europe, it is much more likely that it was "imported" (Jules et al. 2002). Some suspect that it came from the more northerly species of cedar, the Alaskan yellow-cedar, *Chamaecyparis nootkatensis*, which is mildly affected by the fungus, but does not usually die. Although the fungus has never been discovered occurring on Alaska yellow-cedar in the wild, it could potentially be endemic to the area, occurring sparsely on Alaska-cedar trees, and infecting the nursery stock of Port-Orford-cedar when it was cultivated outside of its native range near Seattle, Washington (Zobel et al. 1985). This is not the prevailing view, however. Most believe it has come from Asia, since some of the most closely related *Chamaecyparis* species can be found there, and since the Asian species of *Chamaecyparis* are highly resistant to the *Phytophthora* pathogen (Goheen, Angwin, Sneizko and Marshall 1999).

More than 5000 species of fungi attack plants (Rost, Barbour, Stocking and Murphy 1998), including the species of the genus *Phytophthora*. The name *Phytophthora* means "plant destroyer" (Erwin, Bartnicki-Garcia and Tsao 1983), descriptive of a very large genus of plant-pathogenic fungi. The *Phytophthora* genus includes several other devastating introduced forest pathogens, including *Phytophthora* *cinnamomi*, cause of mortality in a number of the southeastern United States forest trees—such as chestnut and pine—for nearly two centuries (Hansen 1999), and the recently introduced *Phytophthora ramorum*, cause of Sudden Oak Death in California (Hansen 2003). They are water moulds, rather than true fungi, and thus are more closely related to certain types of algae. They produce motile zoospores[4] with the ability to swim a few millimeters in water, seeking out their host plant's fine roots growing in wet soils (Hansen and Lewis 1997). Members of the genus *Phytophthora* exist mainly as hyphae, thin threads of fungus-like material that grow next-to and inside the host plants (FSEIS 2004).

*Phytophthora lateralis* attacks the root systems of trees, rapidly growing up the phloem[5] tissues from the root tips into the root crown and then up the stem, cutting off the root's food supply, killing root cells, and eventually starving the tree of its water source. Usually within a year of the initial yellowing-appearance of the crown, the trees die, their foliage becoming yellow, then brown, and later bronze-colored (figure 4). Before the tree has died completely, the affected phloem tissue can be seen under the bark as dark and reddish-colored (figure 5), contrasting with the white, healthy tissue farther up. One way for the *Phytophthora lateralis* fungus to spread to a new host occurs when masses of these fungal hyphae (known collectively as mycelia) break off or spread along with chunks of their host plant to an uninfected plant. *Phytophthora lateralis* also produces four types of spores, two of which are significant in the spread of root-rot disease. One type of spore, the zoospore, forms when *Phytophthora lateralis* matures,

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[4] Most fungal spores do not have the ability to move; zoospores on *Phytophthora* species differ in this respect.

[5] Sugar transport cells which carry sugars made in the leaves to the tree's roots.

and, usually in the presence of abundant water, these delicate cells with two flagella (FSEIS 2004) are released to swim short distances to new hosts. These zoospores are the most important in spreading the pathogen to new Port-Orford-cedars through streams and saturated soils (Jules et al. 2002). The second important type of spore involved in the spread of root disease is the thick-walled, vegetative chlamydospore. They are more resistant to drier conditions and extreme temperatures. They are capable of either germinating to form mycelia, or, in the presence of water, forming sporangia[6] and then releasing zoospores (FSEIS 2004). These chlamydospores are capable of surviving for at least seven years in the infected remains of roots (FSEIS 2004).

## CURRENT CONDITIONS

### II. Extent of *Phytophthora lateralis* within the Range of Port-Orford-cedar

Most of the information concerning the density and extent of *Chamaecyparis lawsoniana* and the fungal pathogen *Phytophthora lateralis* is from federal lands, as less seems to have been published about the extent of these species on private lands. In the northern portion of its range, near Coos Bay, Oregon, Port-Orford-cedar tends to be more evenly distributed over the landscape, making up a low percentage (usually less than 5%) of stand composition (FSEIS 2004). Since many of these trees grow at some distance from streams or roads, the pathogen has had a relatively low impact in northern locations, Infecting only around 20-30 % of the trees on federal lands even after its fifty-year presence in the area (FSEIS 2004). In locations farther south, spread of *Phytophthora lateralis* has had a more significant effect, since Port-Orford-cedar grows more commonly in rare plant associations, on ultramafic soils, near banks of rivers and lakes.

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[6] Sporangia are structures containing or producing spores.

The Siskiyou National Forest, near the Powers Ranger District, is home to the densest forests of Port-Orford-cedar worldwide, including some unique stands consisting of 70-80 % Port-Orford-Cedar (FSEIS 2004). Of the 61,041 total acres identified to contain Port-Orford-cedar, root disease has reached 8,138 acres, with a few more infected acres appearing in each yearly survey (FSEIS 2004). In the Roseburg BLM District, fewer than 100 of 50,000 acres are infected, while the Medford District contains approximately 2,340 infected acres of the 25,485 acres containing Port-Orford-cedar (FSEIS 2004). In the Six Rivers National Forest, containing the highest proportion of Port-Orford-Cedar on government lands in California, nearly 77% of all Port-Orford-cedar occurs in riparian areas, while spread of the *Phytophthora lateralis* fungus currently covers more than 2,800 acres (FSEIS 2004). Meanwhile, the Biscuit Fire of 2002 reached 499,956 acres of forest in Oregon and California, including nearly 30% of the federal forestlands on which Port-Orford-cedar grows. This included approximately 55,000 acres of uninfected Port-Orford-cedar, as well as 1,400 acres of *Phytophthora lateralis*-infected sites (FSEIS 2004). However, the fire did not kill all the trees within these acres, and when compared with other tree species, a significant portion of Port-Orford-cedar—especially those older trees with thicker bark growing along streams—probably survived.

The future impact of *Phytophthora lateralis* is predicted to vary with region. Those areas considered "high risk" sites[7] are the most likely to become infected (if they are not already) within the next few centuries. The northern-coastal portion of the range

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[7] High risk sites are defined in the Final Supplemental Environmental Impact Statement on Management of Port-Orford-cedar in Southwest Oregon (2004) as "narrow strip[s] along streams affected by water level in the soil profile. Typically this is 10 to 25 feet on either side of the stream channel."

(including Coos Bay and the Siskiyou National Forest), the southern portion (including Klamath, Six Rivers, and Trinity National Forests) and the inland portion (inland portions of Oregon, including Medford and Roseburg BLM Districts), exhibit high risk sites, respectively, of approximately 20%, 40%, and 60% of their lands (FSEIS 2004). Currently, between 76 and 91% of Port-Orford-cedars growing on federal lands still occur on uninfected sites (FSEIS 2004). However, it is within the high-risk sites—primarily lowland, moist areas such as stream banks, river channels, and swamps—that Port-Orford-cedar often has the most important contribution to its ecosystem. Once the pathogen is introduced into these sites, mortality of Port-Orford-cedar is expected to be around 90% within a few years (FSEIS 2004).

Although strategies to prevent spread of the disease have been implemented on federal lands, including closing logging roads during the wet season, washing mud off of heavy machinery prior to entering an uninfected watershed, and eliminating diseased trees from roadside locations, these regulations do not apply to private lands, which contain a significant portion of Port-Orford-cedar. In total, of the approximately 272,000 acres considered to contain Port-Orford-cedar, around 69 % is found on private lands, the remaining 31 % occurring on Bureau of Land Management lands and Forest Service lands (FSEIS 2004). Of these acres, relatively few contain older Port-Orford-cedar larger than 20 inches in diameter, as a significant portion (especially on private lands) has been killed by the root-disease or harvested (FSEIS 2004). Nearly all old-growth Port-Orford-cedar is now found only on federal lands (FSEIS 2004). The Final Supplemental Environmental Impact Statement for Port-Orford-cedar estimates that only 10-20 % of historical old-growth and large Port-Orford-cedar remains within the traditional range of the species.

## II. The Port-Orford-cedar disease resistance breeding program

The Port-Orford-cedar resistance breeding program began in the 1980's, when the USDI Bureau of Land Management and the USDA Forest Service began working in association with Oregon State University, screening trees from natural stands for *Phytophthora lateralis* resistance (*Phytophthora lateralis* Disease Resistance Current Status 2002). Although Port-Orford-cedar trees surviving the disease had been found occasionally in infected stands previous to this time, it was difficult to tell weather they exhibited natural resistance, or had merely escaped infection. In early tests for resistance to the pathogen, all tree cuttings died, suggesting that either the inoculation level of the fungus had been too high, or that resistance, even in surviving trees, was very low (Sniezko and Hansen 1999). Beginning in early 1980's, scientists began working on an inoculation test that might differentiate vulnerable and mildly resistant Port-Orford-cedar (Sneizko and Hansen 1999). Hansen, Hamm, and Roth (1989) eventually found that some degree of resistance to the fungus existed in Port-Orford-cedar. Although the percentage of resistant trees was (and remains) very low, screenings were done of more than 7000 trees from selected potential parent trees throughout the range from 1989 to 1998.

Screening techniques include a branch-dipping inoculation technique, where branches of potentially resistant individuals are either inoculated through an incision cut in the branch, or by dipping cut-ends of smaller branches in a *Phytophthora lateralis* zoospore suspension (Sneizko and Hansen 1999). Seedlings may be screened with the root-dip inoculation test, where two centimeters of their roots are immersed in a zoospore suspension. Cuttings of seedlings are also tested through immersion of the bottom two centimeters of the cutting (Sneizko and Hansen 1999). Following inoculation of dipped branches, the length of growth of the fungus in the roots is measured, with those individuals showing the least growth being considered the most highly resistant (Sneizko and Hansen 1999). After testing of hundreds of branches and clones from selected individuals, certain parent trees stood out as relatively resistant individuals, while many of the other clones showed a low level of tolerance for the pathogen until they were attacked by higher levels of spores (Sneizko and Hansen 1999).

By 2002, through traditional breeding and selection techniques, staff at the Dorena Tree Improvement Center[8] had established families of resistant individuals showing between 0 to 10% mortality in greenhouse testing, as compared to the 80-100% mortality in most Port-Orford-cedar (*Phytophthora lateralis* Disease Resistance Current Status 2002). Also by 2002, more than 10,000 selected individuals had been tested via greenhouse stem inoculation techniques, while 1100 of these were chosen for further breeding and trials (*Phytophthora lateralis* Disease Resistance Current Status 2002). Dorena established its first containerized seed orchards for Port-Orford-cedar. Meanwhile, further screening of previously selected resistant individuals was underway. Field planting sites had also been established within the native range to determine whether resistant trees would show resistance similar to what they had shown in greenhouse trials, and to establish whether they would show long-term resistance.

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[8] Now called the Dorena Genetic Resource Center.

Of the initial 1100 resistant individuals that had been selected in 2002, by 2003 more than 100 were identified as resistant, to be used as parents in the breeding program. Further preliminary testing of greenhouse seedlings found that perhaps 50-75% of trees from the selected resistant parents may survive, versus the approximately 5% survival rate of offspring from vulnerable parents (Port-Orford-Cedar Resistance Testing and Breeding Program 2003). Also in 2003, field plantings from previous greenhouse resistance testing supported previous findings, showing that the same trends in resistance appear in these trees planted in infested sites outside of the greenhouse.

Current breeding and resistance testing of Port-Orford-cedar is ongoing at the Dorena Genetic Resource Center, located near Cottage Grove, Oregon. Goals of the Dorena tree-breeding program include identifying natural resistance in Port-Orford-cedars and producing seed from these individuals through traditional breeding methods. It is hoped that the program will ultimately produce diverse populations of resistant trees adapted to their traditional habitat and range. These individuals could be used to reforest or restore Port-Orford-cedar on high-risk sites—such as riparian areas—where mortality caused by *Phytophthora lateralis* can be particularly high (Port-Orford-Cedar Resistance Testing and Breeding Program 2003). The program currently involves not only Oregon State University, three BLM districts, and five National Forests, but also several local, state, and federal agencies, as well as private land-owners (Port-Orford-Cedar Resistance Breeding Program 2004).

By June, 2004, Dorena Genetic Resource Center had selected and tested 776 new individuals from national, private, and BLM forestlands, bringing the total number of individuals selected for screening throughout the tree's native range to more than 11,000

Port-Orford-cedar (Port-Orford-Cedar Resistance Breeding Program 2004). In addition, seven new field sites for planting resistant trees were added to the 21 previous sites[9] (Port-Orford-Cedar Resistance Breeding Program 2004). The first crops of resistant seedlings grown at Dorena's seed orchards were root-dip tested and planted in some of the field sites. Seedlings from the 2002 seed crop produced by the Dorena resistance breeding program were used in reforestation of Biscuit Fire lands in southwest Oregon, while resistant seed was provided for reforestation in the Siskiyou National Forest (Port-Orford-Cedar Resistance Breeding Program 2004). The Dorena containerized seed orchards were expanded to include seven different breeding zones, established based on elevation and distance from the coast (Port-Orford-Cedar Resistance Breeding Program 2004).

## SPECIES CHARACTERISTICS

**How greatly do similar species of "cedars" differ from the Port-Orford**-cedar? Would it be simpler and more effective to replace Port-Orford-cedar with another species than to breed it for resistance? Would another closely related or associated species even be able to replace most of the Port-Orford-cedar lost within its range? This section outlines the characteristics of the six other *Chamaecyparis* species, as well as discussing other coniferous species native to the range of Port-Orford-cedar. It also describes other significant native and introduced forest pathogens within the range of the Port-Orford-cedar. The impacts of other native forest pathogens are important to the discussion of human responsibilities towards managing these forests, since some insects and fungi cause widespread diseases only after the interference of man in their ecosystems.

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[9] The earliest field site was established in 1989 at Oregon State University.

## I. Species of the genus *Chamaecyparis*

Port-Orford-cedar[10], also known as Lawson Cypress, is a member of the *Chamaecyparis* ("dwarf-cypress") genus, of which there are two other species native to the United States (Alaska yellow cedar, *Chamaecyparis nootkatensis*, and Atlantic white cedar, *Chamaecyparis thyoides)*, and four species native to Japan and Taiwan. *Chamaecyparis*, the "false cypress," or white-cedar genus is a tolerant evergreen tree growing on moist sites, with scalelike, flat sprays of foliage about 1/16" wide. Their cones mature in one season, are small, spherical, and woody to berry-like.[11] The *Chamaecyparis* genus as a whole can be characterized as a water-loving species, occurring in much smaller distributions than most of the dominant conifers, and forming most extensive stands in moist, mid-latitude, mountainous regions in close proximity to coastlines (Zobel 1998). While usually not the dominant species, trees of the *Chamaecyparis* genus tend to out-compete the major dominant species in areas where water limits these other dominant conifers, but encourages the success of the cedar species (Zobel 1998).

The seven species of *Chamaecyparis* are:

*C. lawsoniana*— Port-Orford-cedar, ginger pine, Lawson cypress, Oregon cedar, Lawson cedar;
*C. nootkatensis*—Alaska yellow cedar, Sitka cypress, Nootka cypress, yellow cedar; Alaska cedar;
*C. obtusa*—Hinoki false cypress;
*C. pisifera*—Sawara cypress;
*C. taiwanensis* and *C. formosensis*—the two species of Taiwan; and
*C. thyoides*—the Atlantic white cedar, or southern white cedar (ITIS website 2002).

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[10] Although "cedar" is often used in the common names of *Chamaecyparis lawsoniana*, as well as many of the other members of this genus (and even many other members of the Cupressaceae family), none of these trees are true cedars. True cedars bear evergreen needles borne in clusters, each cluster arising from the branch by means of short woody "pegs," and are members of the Pine family, Pinaceae. There are only three species of true cedars worldwide; none are native to North America.

[11] The genus *Chamaecyparis* is of the kingdom Plantae, the subkingdom tracheobionta (vascular plants), the division Pinophyta (conifers), the class Pinopsida, and the order Pinales. It is a member of the Cupressaceae family, which includes cypress and redwoods (Integrated Taxonomic Information System [ITIS] website 2002).

As one of the geographically closest living relatives to *Chamaecyparis lawsoniana*, the Alaska-yellow-cedar (*C. nootkatensis*) resembles Port-Orford-cedar in appearance as well as range. It has strong, yellowish, aromatic, decay-resistant, valuable wood. Alaska-cedar grows from California through Alaska, growing best in mountainous, rocky or gravelly soils. It is a slower growing tree that has been known to live up to 3,500 years (Griffith 1992). It is medium-sized, averaging 70-100 feet tall and up to four feet in diameter (Jensen, Randall, Keniston and Bever 2002), and rarely growing taller than a shrub at higher elevations (Griffith 1992). In northern parts of the range, Alaska cedar grows down to the shoreline, while further south—within the range of Port-Orford-cedar—it occurs mainly in higher elevations. In the Oregon Cascades it grows mainly between 2000 and 7500 feet (Jensen et al. 2002). Not having evolved the strong physiological traits necessary for competition with other regenerating species in clearings (due either to mortality of young trees or low rates of germination), this species becomes limited in significance in those areas where inaccessibility, snow, and short growing seasons make natural regeneration the most viable form of reforestation following clear-cutting (Dunsworth 1998). While Alaska-yellow-cedar, *Chamaecyparis nootkatensis*, has a similar shade-tolerance, wood quality, and long life-span to Port-Orford-cedar, it tends to grow at higher elevations, infrequently produces good seed crops, produces seeds with a relatively low rate of germination, and is slower growing than Port-Orford-cedar.

On the other side of the North American continent lives the coastally restricted Atlantic white cedar, *Chamaecyparis thyoides*. The Atlantic white cedar is much smaller than the Port-Orford-cedar, growing an average of 40-60 feet tall, reaching as much as 3 feet in diameter, and living an average of 200 years (Tirmenstein 1991). It ranges from northern Florida to Maine, and from the Atlantic and Gulf Coasts westward to southern Mississippi, occurring up to 130 miles inland (Tirmenstein 1991). It is a dominant cover species in some swamps, and has potential as a wetlands restoration species (Tirmenstein 1991). Atlantic white cedar favors swampy conditions, often growing in peat-marshes, along streams, bays, and in moist depressions, and on the stable sides of dunes. It can be found at low elevations along the coast, up to elevations of around 1,500 feet in northern New Jersey (Tirmenstein 1991). It grows well in low nutrient, acidic soils, but does not like clay. It often grows on muck and peat, but also lives occasionally in sandy soils (Tirmenstein 1991). It can potentially live a long time, but is generally a moderately shade tolerant species, disappearing from areas once other species create too much shade. While the Port-Orford-cedar will regenerate in the shade of old-growth forests, the Atlantic cedar relies on disturbance, reseeding quickly following floods and fires. Although both species often survive floods, Atlantic cedar differs from Port-Orford-cedar in that it is very intolerant of fire, even fires of low intensity. Like Port-Orford-cedar, Atlantic white cedar regenerates quickly and thickly when it has the chance, especially on recently burned sites with moist peat soils. The species is interesting in that it relies on fire to clear areas of existing overstory species before its seeds can germinate, while fire is usually fatal to the trees themselves.

Unlike Port-Orford-cedar, the Hinoki tree, *Chamaecyparis obtusa*, of Japan, prefers moist, well drained sites in full sunlight, in moderate to high humidity, sheltered from strong winds. In its native habitat of Japan, it reaches more than 120 feet tall, with a tall, straight trunk and narrow, pyramid-like crown. Both the Hinoki cypress and the

Sawara cypress (*C. pisifera*) grow in southern and central Japan, mainly in mountainous areas, and occasionally in the same stands (Zobel 1998). Hinoki cypress tends to occur on the higher reaches of slopes and ridge-tops, while Sawara cypress prefers wetter, more shallowly sloping land. Generally, the Hinoki cypress grows in regions with the highest seasonal climatic variation among the ranges of *Chamaecyparis* species (Zobel 1998), while the Taiwan cypress grows in the region with least variation.

## II. Other Dominant Conifer Species Native to the Range of Port-Orford-Cedar

The Port-Orford-cedar grows in association with many other conifers, which are mainly evergreen needle-bearing trees of the family Pinaceae. These include spruce, hemlock, Douglas-fir and true fir, as well as pines. Sitka spruce, western hemlock, Douglas-fir, and grand fir are common in the coastal and central areas of the Port-Orford-cedar's range, while pine and true firs are more common in higher elevations. In eastern portions of its range, white fir, white pine, Shasta red pine, and mountain hemlock are common. It grows in association with tanoak and redwood in the more southern extents of its range.

Sitka spruce is a large coniferous tree, bearing spirally arranged, sharp needles, with an average height of 125-180 feet and diameter of three to five feet (Jensen et al. 2002). Sitka spruce bark is somewhat thin, usually less than an inch thick, making them less resistant to fire than Port-Orford-cedar. They prefer damp, coastal, well-drained sites, seldom growing as far as 50 miles inland or above 1,800 feet in Oregon (Jensen et al. 2002). They range from Alaska to northern California along the coast.

Douglas-fir is the most common and widely planted timber species of the Pacific Northwest. It is a large tree, sometimes reaching more than 250 feet tall or six feet in diameter, bearing soft, spirally arranged evergreen needles, and having thin bark as a young tree, which thickens to as much as ten inches thick near the base of old trees (Jensen et al. 2002). It grows on a variety of soils from Alaska to Mexico, from the Rocky Mountains to the coast; like the Port-Orford-cedar, it ranges up to 5,000 feet along the coast (Jensen et al. 2002). Of intermediate tolerance as a seedling and growing less tolerant as it matures, Douglas-fir is much less shade-tolerant than either the Port-Orford-cedar or western hemlock.

Western hemlock is a very shade-tolerant species throughout its life. Its seedlings often regenerate on nursery logs in the shade of old-growth forests, where few other young canopy species are able to survive without the light from some sort of gap in the canopy. Western hemlock is a large tree, reaching 150-200 feet tall, two to four feet wide, with thin bark up to an inch thick on old trees, and bearing short evergreen needles. Preferring deep, moist soils, they range from Alaska to northwest California, inland as far as northern Idaho, and up to 6,000 feet above sea level in Oregon (Jensen et al. 2002). Its high-elevation counterpart, the mountain hemlock, is similarly shade-tolerant and thin-barked, and occurs in association with Port-Orford-cedar at high elevations. While, like the Port-Orford-cedar, they are very tolerant of shade, their thin bark makes them much more susceptible to fire damage, even as older trees.

Grand fir, *Abies grandis*, a large tree, rivaling Douglas-fir in height and diameter, of less shade-tolerance than western hemlock, is the only true fir in Oregon found at sea-level (Jensen et al. 2002). It prefers moist conditions in valleys and on mountain slopes up to 6,000 feet above sea level, on the west side of the Cascades, from British Columbia into northwestern California (Jensen et al. 2002).

The more mountainous species of true firs include Pacific silver fir, white fir, grand fir, subalpine fir, red fir, and noble fir. Pacific silver fir, *Abies amabilis*, is a smaller, moderately tolerant, higher-elevation fir species growing on well-drained gravelly and sandy soils between 1000 and 6500 feet in elevation in Oregon (Jensen et al. 2002). It grows in association with most of the above species at mid-elevations, as well as with pine and spruce at higher elevations, and will germinate seeds on both duff and mineral soils (Jensen et al. 2002). White fir, *Abies concolor*, generally grows higher than 3000 feet, is shade-tolerant, prefers drier, coarse soils, and has thick bark near the base of older trees which is somewhat resistant to fire (Jensen et al. 2002). Noble fir, *Abies procera*, is a shade-intolerant, less fire-resistant fir growing in the mountains between 1400 and 6000 feet in elevation. California red fir, *Abies magnifica*, grows above 4000 feet, is of intermediate shade tolerance, and prefers well-drained, moist, subalpine soils (Jensen et al. 2002). Subalpine fir, *Abies lasiocarpa*, is a small subalpine tree, growing at high elevations of 2100-7800 feet in Oregon.

Also growing at higher elevations are the pines, which range from intermediate shade tolerance to preferring full sun. Both western white pine, *Pinus monticola*, and sugar pine, *Pinus lambertiana*, are larger pines, occurring above 2000 feet in elevation, on a variety of soils in the mountains. Jeffrey pine, *Pinus jeffreyi*, grows on many soils, preferring gravelly and sandy sites—although also growing in serpentine soils, in the southern Cascade Mountains of Oregon, into California, between 3000 and 9500 feet in elevation. Ponderosa pine, *Pinus ponderosa*, as well as lodgepole pine, *Pinus contorta*, are very widespread, commonly found on sandy, gravelly soils. They grow on many different types of soils and under varying soil conditions, both at low elevations, and in the mountains. Ponderosa pine tends to grow on dryer soils than lodgepole pine—which is found in coastal dunes, swamps, and bogs.

Two other more closely related native species similar in appearance to Port-Orford-cedar are the incense-cedar, *Calocedrus decurrens*, and western redcedar, *Thuja plicata*. Both of these species are in the same family as Port-Orford-cedar—Cupressaceae (which includes cypress and redwoods), share similar scale-like foliage, and have straight-splitting, light, aromatic wood.

Incense-cedar (*Calocedrus decurrens*) has thick, fire-resistant (in older trees), furrowed bark and scale-like flattened sprays of foliage similar to that of Port-Orford-cedar. It prefers porous, damp soils, but is less moisture-dependent than *Chamaecyparis lawsoniana*, growing on both sides of the Cascade Mountains in Oregon, as well as all along the Sierra-Nevada Mountains in California (Jensen et al. 2002). It ranges in elevation between 1,000 and 6,000 feet in Oregon, and up to as much as 75,000 feet above sea level in the most southerly extent of its range in California (Jensen et al. 2002). It often withstands fires that kill its thinner barked associated species, and regenerates well following disturbance. As a rather drought-resistant species and prolific seed producer, it would be more prominent in southern Oregon and northern California forests if it were not such a slow-growing species (Jensen et al. 2002).

Western redcedar, *Thuja plicata*, is a native species to the Pacific Northwest, somewhat similar in appearance to Port-Orford-cedar. While it is of a different genus, western redcedar, *Thuja plicata,* has similar scale-like foliage, thick bark, and aromatic, straight-splitting wood to that of the Port-Orford-cedar. It is the largest tree of its genus, sometimes reaching 200 feet tall and ten feet in diameter (Jensen et al. 2002). It occupies approximately the same southern range as Port-Orford-cedar, as well as extending much farther northwards. Western redcedar also prefers moist, protected habitats, but does more poorly on nutrient-poor ultramafic soils. In a comparison of soils from these two species, Imper and Zobel (p. 1226, 1983) found that Port-Orford-cedar "often is more dominant on less-fertile ultramafic soils, in which availability of N and Ca, and the Ca:Mg ratio, are usually relatively low." They also found that soils were relatively fertile in locations where the two species were intermixed, whereas Port-Orford-cedar was much more abundant on serpentine, or ultramafic, soils.

## III. Other Northwest Forest Pathogens

Many other fungal pathogens attack forest trees or certain species in the Pacific Northwest. Some of the most widespread and well-known within the range of Port-Orford-cedar include Swiss needle cast, white pine blister rust, sudden oak death, and laminated root rot. In addition to fungal forest pathogens, several insects, including the Douglas-fir tussock moth, spruce budworm, and pine beetles attack trees within Port-Orford-cedar's range.

Swiss needle cast of Douglas-fir trees, caused by the fungus *Phaeocryptopus gaeumannii,* has been a problem mainly in areas where large plantations of Douglas-fir trees were planted near the coast, such as Christmas tree farms and replanted cleared areas. In 2002, over 385,000 acres of Douglas-fir were found to be moderately or severely impacted by the fungus (Filip 2002). In an aerial survey done in 2003, nearly 270,000 acres were found to be infected (Kanaskie, McWilliams, Sprengel and Overhulser 2003). The disease was first identified in North-American Douglas-fir planted in Switzerland in 1925. A survey 14 years later found the fungus present in most North American and Canadian forests at non-epidemic levels (Filip 2002). It was not until the 1970's that Swiss needle cast became a problem in Christmas tree plantations, and not until the 1980's that the disease became significant in forest plantations (Filip 2002). It is mainly a problem in trees growing under stressed conditions, and where seeds imported from a drier location have been planted in wetter conditions with warmer winters, such as nearer to the coast and on south-facing slopes. The fungus *Phaeocrytopus gaeumannii* parasitizes the stomata of its host, infesting mainly the newer needles, and causing premature needle loss[12] in trees under stress, unnatural growing conditions, or during especially wet years. Unless an especially large amount of needles are lost, trees remain relatively healthy, although they may not grow as quickly.

Laminated root rot, *Phellinus weirii*, a widespread endemic pathogen of northwestern forests, attacks many conifer species. There are two different forms of *Phellinus weirii* present in western North America, one affecting Douglas-fir, spruce, and true firs (and occasionally pines, which are resistant, but not immune), and a second form causing butt-rot in western redcedar (*Thuja plicata*). Hardwoods are immune to laminated root rot. The disease spreads via mycelia to new trees, through roots of previously infected logs or stumps. Rather than relying on spores, the fungus mainly acts clonally, as large, sometimes ancient, vegetatively propagating individuals spread slowly

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[12] Needles are normally retained for up to seven years.

through the forest (Hansen and Goheen 2000). It begins growing in the xylem, degrading both lignin and cellulose, eventually killing the tree, and then living as a saprophyte off the dead tree for many years. It has been known to survive for over fifty years in old-growth logs (Hansen and Goheen 2000). The pathogen spreads slowly outwards from an infection center, creating rings of progressively dying and dead trees in circular patches. These patches range from small clearings to several acres in diameter, depending on availability and proximity of host species. From an economic standpoint, this root disease is one of the most destructive in Oregon (Hansen and Goheen 2000). Several other root decay diseases are caused by fungi—armillaria root disease (*Armillaria ostoyae*), annosus root disease (*Heterobasidion annosum*), and black stain root disease (*Leptographium wageneri*)—although they are less significant from an economic standpoint. As a group, most of the endemic root rot fungi are important in creating more diverse types of habitat in the forms of decayed or hollowed out logs and stumps, clearings in the canopy, and altered tree species and age compositions.

Sudden oak death, an exotic pathogen that has wiped out many Californian oak forests, was recently found on tanoak in southwest Oregon. It is caused by another *Phytophthora* species, *Phytophthora ramorum*. The sudden oak death disease was relatively recently described. Soon after the symptoms were recognized and attributed to this disease, in 1994-1995, the disease caused widespread damage in central coastal Californian oak forests, attacking species of tanoak (*Lithocarpus densiflorus*), California black oak (*Quercus kelloggii*), coast live oak (*Q. agrifolia*), and Shreve's oak—*Q. parvula* var. *shrevei* (Rizzo 2003). Many other species aside from oak, throughout both Oregon and California, were also found to be possible hosts to the disease (Rizzo 2003).

Symptoms vary in manner and severity from one species to another, with foliar spots, branch dieback, and wilts on Douglas-fir, *Pseudotsuga menziesii*, coast redwood, *Sequoia sempervirens*, big-leaf maple, *Acer macrophyllum*, California bay laurel, *Umbellularia californica*, evergreen huckleberry, *Vaccinium ovatum*, and madrone, *Arbutus menziesii* (Hosts and Symptoms 2003). Oozing cankers on the bark that "bleed" burgundy-to tar-colored sap are found in tanoaks, *Lithocarpus densiflorus*, black oaks, *Quercus kelloggii*, and coast live oaks, *Quercus agrifolia* (Hosts and Symptoms 2003). Since this pathogen infects such a variety of species (even though it has been found to cause mortality in relatively few of them), a more diverse forest composition may actually help rather than hinder the spread of the pathogen from one tree to the next (Rizzo 2003).

The white pine blister rust has two alternating hosts—currants and gooseberries (*Ribes* spp.) and five-needled or soft pines (*Pinus* spp). It attacks only the five-needled members of the Pinaceae family—sugar pine, western white pine, eastern white pine, whitebark pine, limber pine, and Swiss stone pine—and is caused by the rust fungus *Cronatium ribicola* (an exotic pathogen to both Europe and North America). White pine blister rust was "imported," most likely from Asia or Europe, near the beginning of the twentieth century, also following the nursery trade. During that time it was more economic to import white pine seedlings from Europe than to grow them in the United States, hence French and German white pine seedlings were shipped to America. First identified in 1906 on a species of currant in New York, it had a great impact on the eastern white pine, which was an important timber species at the time. *Cronatium ribicola* has now spread nearly everywhere throughout the range of five-needled pines of North America. During the fall, *C. ribicola* spores produced on the *Ribes* host are released, blown by the wind to their second host, a five-needled pine. The rust fungus then enters pine leaves through stomata, growing into the leaves, twigs, branches, and eventually (although not always) reaching the trunk of the tree. It grows in this way through the phloem and bark tissues for two to three years without symptoms, before cankers begin to form and develop (Blanchard and Tattar 1997). These yellowish-brown cankers grow around and eventually girdle the branches or trunk of the tree, killing the branch or crown above it. Western white pine now occupies somewhere around 5 % of its original range, partially due to this pathogen (Hansen and Goheen 2002; Ripley 2002). White pine blister rust has consequently altered ecosystem response to endemic root rots, since the western white pine was one of the important, long-lived, tall-growing, laminated-root-rot-resistant trees to colonize gaps left by the root rot.

Several insect species also deserve mention as "pathogens," since they sometimes reach epidemic infestation levels that kill larger trees as well as those of reduced vigor, especially in dense stands where other natural disturbance events such as fire have been suppressed. Phytophagous insects include Douglas-fir tussock moths, bark beetles, flatheaded fir borers, Douglas-fir beetles, Pandora moths, and fir engravers. Some insects usually cause little harm unless their population size reaches a certain level. The mountain pine beetle, *Dendroctonus ponderosae*, infests lodgepole pines, ponderosa pines, western white pines, and sugar pines, as well as other species of pine and some exotic species present in the pine beetle range. As endemic smaller-sized populations, the pine beetles usually attack only young or damaged trees, but when their populations reach high numbers, they attack the more resistant, larger-diameter, older pines. Defoliating insects also have the ability to cause widespread damage. For example, in ponderosa pine stands of Klamath County, more than 24,000 acres were defoliated by Pandora moths in 2002 (Ripley 2002). Both native and nonnative forest insects and fungal pathogens vary in intensity and impact from year to year. They depend on a complex interaction of ecological, physical, and biological factors that are, in turn, influenced greatly by humans' involvement in the ecosystems.

## ECONOMIC AND ECOLOGICAL ISSUES

Port-Orford-cedar provides many specialized and significant contributions to both its associated forested and aquatic communities. Local adaptations to specific soils, sites, and plant associations are also unique in each of the *Chamaecyparis* species, as well as among other native Northwest conifer species. Perhaps several of these species may together be able to replace some of the ecosystem functions or economic significance attributed to the Port-Orford-cedar, although no single species is likely to entirely replace it. The specific growing conditions which make Port-Orford-cedar vulnerable to contacting such a pathogen are also some of the characteristics which make its ecological role unique and important to the ecosystem. This section further discusses some of the ways ecosystems and cultural values may be influenced by loss of the Port-Orford-cedar, compares *Phytophthora lateralis* with other native and non-native forest pathogens within the same geographical range, and leads into the discussion about the significance of breeding *Phytophthora lateralis* resistant Port-Orford-cedar.

## I. Ecological and Biological Contributions of Port-Orford-Cedar to its Ecosystem

Watersheds of the Pacific Northwest receive a great amount of rainfall during the fall, winter, and spring months, most of which can be absorbed into the ground under naturally forested conditions. This rainfall is caught and held in the canopy, leaves, ground-covering shrubs and herbs, accumulation of decomposing twigs and needles on the forest floor, the soft organic layer of decomposing matter, and throughout the soil. It takes a much longer amount of time for all this water to filter through the watershed and enter streams and rivers than it would without the forest's dense, water-holding canopy and associated under-story species. Forested watersheds therefore act as a filter, reservoir, and regulator of water in watersheds. They prevent major floods from occurring when it rains continuously for a few consecutive days, hold the soil together in the presence of large amounts of water, and shelter streams from large amounts of sediment. They also support a much more consistent water flow, allowing more water to slowly percolate into the stream channel from groundwater during drier months. In logged or burned areas, buffer strips of trees and shrubs left along the water channels are important in protecting the streams from excessive runoff, debris, and sediment. These trees provide clearer, cleaner water in the channel itself, while shading the channel and decreasing summer water temperatures. In such situations, Port-Orford-cedar can be important as a cover species, since it is both a climax-community species and a water-loving species.

Cover species such as Port-Orford-cedar are particularly important in those riparian habitats where they provide cover and in-stream structure for steelhead and coho salmon, especially during spawning season and for maturing salmon. Salmon have very different habitat needs during different parts of their life cycles. They require certain ocean conditions, specific pH levels, oxygenated and gravelly spawning conditions, cover, and specific temperatures. In-stream structures, such as the presence of gravel, undercut banks, shade, bends, and pools for resting are also crucial. Cedar and other streamside plant species are important in maintaining many of these conditions.

Young salmon generally need a freshwater habitat with shelter, lower water velocity, and food. When excessive soil and debris runoff leaches into the spawning areas, it can clog young fishes' gills, kill insects they feed on, and increase water temperatures. Fish also have very specific requirements for spawning. Some require debris—such as twigs, banks, mud—to attach their eggs to; other species (such as salmon) build nests out of cobble or gravel. Large woody debris—such as downed cedar logs—are important in-stream structures for trapping and holding gravel and cobble, making it possible for several species of fish to be able to dig their deep nests or trenches necessary for spawning. These downed logs are also important in slowing down the water velocity to protect the eggs. Also of great importance to stream habitats are pools and riffles[13]. Riffles are extremely productive habitats for aquatic insects, which in turn provide food for young salmon, while pools and undercut banks provide shelter and resting areas for salmon. Downed Port-Orford-cedar logs and branches—since they often grow in close proximity to streams—may be important in creating these structures. Due to their longevity in streams, Port-Orford-cedar logs and downed branches provide long-

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[13] Shallow, ripple-filled areas.

term diverse habitats, not only for salmon, but for various reptile and amphibian species, as well.

The importance of Port-Orford-cedar within watersheds is not limited to ground-cover or structural diversity within stream channels. Since it "often grows within the active stream channel" (Hansen, Goheen, Jules, Ullian and Sutton 1999), Port-Orford-cedar also contributes to aquatic ecosystems by controlling erosion, stabilizing banks, and protecting channel structure (Jimerson 1999). Cover over the channel itself is also very important, since it helps keep water cool during the summer time, maintaining the narrow range of in-stream temperatures in which salmon can comfortably survive (FSEIS 2004). In those ecosystems more prone to fires, Port-Orford-cedar is among those species with thick, fire-resistant bark that enables them to survive most fires and provide crucial stream-cover while other species are recovering following burns.

Port-Orford-cedars are of significant value on serpentine soils, where the low ratio of calcium to magnesium makes it difficult for many other trees to grow (Jimerson 1999). These serpentine soils are developed from weathered ultramafic igneous rocks, which are typically composed of high amounts of iron, magnesium, manganese, nickel, cobalt, and chromium, with much lower levels of silica, calcium, and aluminum than other forest soils (FSEIS 2004). Port-Orford-cedar is one of the few forest species to tolerate this heavy mix of clays and minerals (FSEIS 2004). Some of these compounds are toxic for many plants; certain nutrients such as nitrogen, phosphorous, and potassium are at lower than needed levels, and the low calcium to magnesium ratio further eliminates many plants from growing (FSEIS 2004). Several other unique, native, and rare plants grow in these soils. Port-Orford-cedar may also be found growing in association with Jeffrey pine, western white pine, and tanoak in these locations, where it makes up an average of 50 % of the over-story in riparian sites, and around 38 % in upland locations (FSEIS 2004).

Because of the diversity of habitats and geographic regions Port-Orford-cedar grows on, it also grows in association with a great diversity of plant species. It has been found growing with 29 other overstory species, 93 species of shrubs, and 446 herb species (Jimerson 1999). It grows in association with at least 30 rare, sensitive, and "special status" species, including 11 species found only within Port-Orford-cedar plant associations (FSEIS 2004). Rare species growing in association with Port-Orford-cedar on serpentine wetlands include the California pitcher plant, *Darlingtonia californica*, California Lady's slipper, *Cypripedium californicum*, western bog violet, *Viola primulifolia* var. *occidentalis*, and waldo gentian, *Gentiana setigera*. In wetlands, both the large-flowered rush lily, *Hastingsia bracteosa*, and Oregon willow herb, *Epilobium oreganum* are found growing with Port-Orford-cedar, while Scott Mountain phacelia, *Phacelia dalesiana*, showy raillardella, *Raillardella pringlei*, and crested potentilla, *Potentilla cristae*, are all found with Port-Orford-cedar in the Scott Mountains of California (FSEIS 2004).

## II. Importance of Ecological and Biological Differences between Port-Orford-Cedar and Other Similar Significant Coastal Forest Species

Port-Orford-cedar differs from many of its associated species in both fire and shade tolerance. When compared with the other dominant coniferous timber species occurring within its range, Port-Orford-cedars have moderate shade tolerance, being more tolerant than incense-cedar, *Calocedrus decurrens,* and Douglas-fir, *Pseudotsuga menziesii*, but less shade-tolerant than the western redcedar, *Thuja plicata*, western hemlock, *Tsuga heterophylla*, or spruces, *Picea* spp. (FSEIS 2004). Port-Orford-cedar can survive and reproduce well in the shade, perhaps better than all the other species except for western hemlock (FSEIS 2004). Capable of surviving repeated fire, Port-Orford-cedar may withstand fires even as pole-sized trees. Often the first species to reestablish following a burn, Port-Orford-cedar is more successful at surviving fire than most other species (including western hemlock and true firs) except for Douglas-fir (FSEIS 2004).

While Port-Orford-cedars grow in a variety of land surfaces, soils, and locations, they are not very tolerant of drought, (although more drought-tolerant than western hemlock and Sitka spruce), and their range is probably limited by abundance of water. Although they grow better on other soil types (FSEIS 2004; Jules et al. 2002), Port-Orford-cedars are particularly well adapted to ultramafic soils, on which they can out-compete most other competitors. Immune to the laminated root rot disease, they are found recolonizing patches left by this fungus in the Siskiyou Mountains of Southwest Oregon (Hansen and Goheen 2000).

As compared with many other western North-American conifer species, Port-Orford-cedar tends to be more closely associated with lower-elevation, coastal streams of southern Oregon and northern California. Also, Port-Orford-cedar wood decays much more slowly within stream channels than many common native species such as spruce, Douglas-fir and hemlock. Port-Orford-cedar therefore provides important cover and structure for the channel—keeping water temperatures cool, maintaining stability on river banks, influencing the channel shape and substrate, and adding pools and complexity (via fallen logs and branches) to in-stream habitat. All of these channel features are important for the conservation of salmon habitat, as well as the other aquatic and forest species associated with salmon.

Although many other native species are well adapted to the growing conditions within the native range of Port-Orford-cedar, most have significant differences in elevation range, soil requirements, or moisture preferences, preventing them from completely replacing Port-Orford-cedars in habitat and function. They also differ in shade and fire tolerance, affecting their role as important species in both very old, as well as very young forest stands. Many are susceptible to other native or introduced forest pathogens, and many cannot grow in such close proximity to streams on ultramafic soils (FSEIS 2004). While many other native conifers have wood of high economic significance, few have the characteristically decay-resistant, aromatic, straight-splitting wood of the Port-Orford-cedar.

Of the two native species with wood closely resembling that of the Port-Orford-cedar, the incense-cedar, *Calocedrus decurrens*, is a rather slow-growing tree, while the western redcedar, *Thuja plicata*, is less well-adapted to low-nutrient, ultramafic soils. The western redcedar, a native species to the Pacific Northwest and in the range of Port-Orford-cedar, shares a similar economic value and cultural significance. While also preferring moist habitats, it does more poorly on nutrient-poor ultramafic soils. Based on observations of soil nutrients within the study site where both species were growing, Imper and Zobel (1983) concluded that, "given the apparent nutritional requirements of *Thuja*, it seems unlikely that it will significantly replace *Chamaecyparis* killed by root rot." The Incense-cedar, *Calocedrus decurrens*, another slow-growing, fire-resistant, "cedar-like" species, found within the range of the Port-Orford-cedar, occurs in more mountainous locations and is less rot-resistant than its relatives, trees of the *Chamaecyparis* genus. It is susceptible to a heartwood-attacking fungus, lowering its value as an important lumber species (Jensen et al. 2002).

Port-Orford-cedar also differs significantly from other species of its own genus, having unique ecological and biological characteristics well suited for conditions within its native range. When compared with the other species of *Chamaecyparis* discussed in the previous section, Port-Orford-cedars are abundant seed producers, quick-growing seedlings (FSEIS 2004), shade tolerant (Jensen et al. 2002), fire and flood-resistant, and the best adapted to many of the local soils and climatic patterns within their native range. As the largest member of the *Chamaecyparis* genus, the Port-Orford-cedar grows well both on ultramafic, poor soils, and in very wet conditions. It occurs in a variety of coastal plant associations, serving an important role in the climax communities on stream banks and in swamps. It is unlikely that any of the other trees of this genus would grow as successfully or prolifically in those areas where contribution of Port-Orford-cedar to the community is needed the most. This may be especially true in ultramafic, low-elevation, fire-prone watersheds, where the Port-Orford-cedar contributes shade and large woody debris to the aquatic habitat. There is also the possibility that introducing a non-native tree species would bring additional exotic fungal or insect pathogens along with it.

## III. Economic and Cultural Importance amongst False-Cedars and Other Native Northwestern Species with Similar Wood Characteristics

Trees of the *Chamaecyparis* genus, all of which are found in coastal environments, have characteristically light-colored, decay-resistant, easily workable, relatively strong wood that usually finishes well and has been valued as a timber species in local economies (Zobel 1998). Currently, most of the demand for *Chamaecyparis* wood is in Japan (Zobel 1998), where its unique aesthetic properties—oils, straight grain, fine color and decay resistance—are especially valued. However, the economic, cultural and social values of this species are also important to the Pacific Northwest.

Alaska-yellow-cedar, *Chamaecyparis nootkatensis*, occurs in locations much closer (ecologically, as well as geographically) to Port-Orford-cedar than any of the other species of the genus. Alaskan-Yellow-cedar's wood has been used to build dug-out canoes and canoe paddles by Native Americans. Its bark was used for clothing and weaving, the leaves used for sweat-baths and medicinal purposes. Its strong, aromatic, decay-resistant, bright-yellow wood is probably the most valuable of Alaskan trees, being used for boat-construction, canoe paddles, furniture and interior finishing, cabinets, fences, saunas, and musical instruments (Jensen et al. 2002; Hennon, Shaw, and Hansen 1998). It is a valuable export species, especially to Japan, where they use it in construction of houses, temples, and shrines (Hennon, Shaw and Hansen 1998). Despite this, the species is currently dying, for unknown reasons, in many of its unmanaged forest stands in southeastern Alaska (Hennon et al. 1998). This widespread mortality, unique among the Alaskan forests to the *C. nootkatensis* species, has devastated some 200,000 acres of Alaskan forest in the last hundred years. Current evidence suggests that climatic warming over the last century is the most likely cause of this decline (Hennon et al. 1998), so the species is not likely to suffer from the same causes of mortality in other parts of its range. While it is successful at growing on extremely poor soils and in high-elevations, this species is usually limited by a relatively short growing season, and can be one of the most slow-growing of the conifers in North America. Harris (1971) has recorded ring-widths as narrow as 2 rings per millimeter in Alaska cedar wood. Because it is a much less prolific reproducer, as well as a slower-growing species restricted to mountainous regions of southern Oregon, *Chamaecyparis nootkatensis* is less valuable as a commercial timber species in the lower elevations within the range of Port-Orford-cedar.

The Hinoki cypress, *Chamaecyparis obtusa*, is also of significant economic value. Because of the strength of its wood, it is used in construction for foundations and columns. It is also used to build beautiful, aromatic, long-lasting wood tubs (Bartok Design co. Website 2003). The sweet, lemon-scented, light-colored wood has a straight, compact, rich grain, and a natural resin which discourages rot or insect attack. Similarly, the Sawara cypress, *C. pisifera*, has a straight-splitting, weather and humidity-resistant wood, which is often used in siding, roof frames, and floors. These two species are of high demand and limited supply in Japan, where the Port-Orford-cedar is sometimes used to replace them.

Port-Orford-cedar wood, considered one of the most highly valued conifers of commercial timber species worldwide, has often been sold at ten times the value of Douglas-fir lumber harvested from the same locations (Hansen, Goheen, Jules and Ullian 2000). Its straight-grained decay-resistant wood has been used in construction of boat hulls, as arrow-shafts and Venetian blinds, and in battery-separators, a market largely taken over by other products (Hansen et al. 2000). There has been a steady decline in the amount of Port-Orford-cedar wood exported annually since the early 1960's—an estimated sixty million board feet were exported annually from the U.S. during the 1960's (Barnes 1999). However, Port-Orford-cedar is still popular locally, not only for its wood, but also for its oils, branches, and ornamental varieties. From the early to late 1990's, export volumes dropped from 11 million board feet per year to around two million board feet per year (Barnes 1999), with the export values dropping respectively from 29 to 6.5 million dollars. At the same time, local usage of the wood increased from 2.5 to 6.5 million board feet (Barnes 1999). The wood is presently used for straight, light-weight, durable arrow shafts, woodworking, construction of sacred buildings, sailboats, sweat-lodges and saunas, and many other uses. Boughs and branches are collected year round, dyed various colors, and used by the floral industry to be made into wreaths, garlands, and as decorative greens (FSEIS 2004). The floral industry brings in around $1.5 million a year from bough collections (Barnes 1999). Port-Orford-cedar's total contribution to the local economy, in the form of lumber, arrow shafts, floral greens, and employment related to Port-Orford-cedar is around $14 million per year (Barnes 1999).

The demand for wood of similar quality to Port-Orford-cedar could partially be filled by the two other similar native species common in Southwest Oregon, the western redcedar, and the incense cedar. Western redcedar, *Thuja plicata*, shares a similar economic value and possibly an even greater cultural significance than the Port-Orford-cedar. Its wood is resinous, decay-resistant, sturdy, and straight-splitting. It has traditionally been used by the Native Americans in construction of buildings and sweat-lodges, canoes, and totem poles, while its bark has been used in making their basketry, mats, rope, twine, hats, and clothing (Gonzalez 2004). The wood is currently used in construction of roofs, decks, saunas, fences, door and window-frames, planters, paneling, siding, and many other items, from furniture to musical instruments (Gonzalez 2004). It is estimated that 903 million board feet of western redcedar was harvested in 2002 in British Columbia alone (Gonzales 2004). Although having somewhat different growing preferences from those of the Port-Orford-cedar, the western redcedar remains resistant to most highly destructive forest pathogens, and will likely continue to be of economic significance within the Port-Orford-cedar range. Although less decay-resistant, and subject to particular heart-decay fungi, the wood of incense cedar, *Calocedrus decurrens* is also sturdy, pleasant-scented, and valuable. Its durable wood makes exceptional fence-posts, while it is less-frequently used for cedar chests, stakes and shakes, blinds, ties, and lumber. It has also been the main species used to make pencils (Jensen et al. 2002).

## IV. Growing Preferences of Port-Orford-Cedar Which Make Them, Specifically, Vulnerable to Contacting This Pathogen

Few other species of insect or fungal pathogens attack the Port-Orford-cedar. Some may become infested with amethyst cedar borers (*Semanotus amethystinus*) or cedar bark beetles (*Phloeosinus* spp.), which are rarely responsible for killing Port-Orford-cedar trees without outside causes, and which usually only infest vulnerable or stressed trees (Goheen, Angwin, Sneizko and Marshall 1999). Black bears may occasionally peel off the bark of trees in the early spring to feed on the cambium, sometimes girdling and killing Port-Orford-cedars (Goheen et al. 1999). Some other varieties of fungi besides *Phytophthora* have been found on Port-Orford-cedar (such as *Phellinus pini* and *Heterobasidion annosum*), but most do not appear to strongly affect the tree (Goheen et al. 1999). Meanwhile, *Phytophthora lateralis* began destroying almost all Port-Orford-cedar it came in contact with, acting as an extremely virulent pathogen only to this one particular species of tree.

*Phytophthora lateralis* is known only to infect one other tree in the wild (Pacific yew, *Taxus brevifolia*), and that species is rarely infected unless it is growing in close association with infected Port-Orford-cedar trees (Goheen et al. 1999). This fungus is very well adapted to spread in water, an adaptation that mirrors the preferences of its coastally restricted host species. The production of zoospores and the development of sporangia are more successful in the moist, cool coastal conditions of the host species' range. The mobile zoospores are capable of swimming for several hours in still water, and can travel even further in flowing waters (Goheen et al. 1999). These swimming spores can detect root exudates of Port-Orford-cedar and follow this until finding live root tissue, penetrating it, and germinating (Goheen et al. 1999). Port-Orford-cedar often have an abundance of shallow, small rootlets in the upper layer of the soil, which may be only partially covered in soil, and this is where most infection initially occurs (Goheen et al. 1999).

The fungus can proliferate rapidly when there is an abundance of host plants to colonize, but it is also able to remain dormant for considerable lengths of time awaiting conditions more conducive to spread or infestation via its zoospores (A Range-wide Assessment of Port-Orford-Cedar 2003). In less favorable moisture or temperature conditions, the pathogen may form chlamydospores on the roots it currently infects, which may remain dormant until better conditions for infection develop, such as following a summer drought. The pathogen can survive this way for seven years or more (Goheen et al. 1999) in roots and debris of previously infected trees. These resting spores can germinate to produce more zoospores when conditions are favorable again.

While water and the site preferences of Port-Orford-cedar play a significant role in the success of this pathogen, humans are one of the main vectors contributing to the ease of spread of the disease. Transportation of infected soil, wood, or mud, weather through road construction, logging operations, mining, or traffic, have been the main reasons why the disease spread. Foot traffic—from soil carried on the hooves of cattle, elk, deer, or the feet of humans—acts as a much more local, small-scale means of spread (Goheen et al. 1999). The disease can also be spread through transportation of infected seedlings and from root grafts of infected-to non-infected trees.

## V. Native versus Introduced Forest Pathogens in the Range of Port-Orford-Cedar.

Some native forest pathogens increase primary productivity by speeding up nutrient and energy cycles, as they weed out the stressed, dead and dying trees or vulnerable branches, speed decay and recycling of nutrients, create snags, and leave more room for healthy trees (Schowalter, Hansen, Molina and Zhang 1997; Ripley 2002). Many beetle infestations, as well as various types of decay fungi, help in these processes. Other endemic pathogens affect larger, more vigorous trees, creating clearings or patches within an often dense, primarily coniferous canopy. These types of pathogens—such as the laminated root rot—create more structural diversity, as well as changing species diversity (Schowalter et al. 1997; Hansen and Goheen 2000). In older coniferous forests less prone to fire, the laminated root rot may clear spaces for more early successional species, such as hardwoods and shade-intolerant shrubs. Still other pathogens—such as phytophagous[14] insect species and perhaps the fungus responsible for Swiss needle cast—have existed in the Pacific Northwest forests as endemic, low-impact parasites for hundreds of years.

In some instances, such as with the recent increase in Swiss needle cast damage, misunderstandings in management techniques, as well as physical changes in the environment, encourage the proliferation of endemic forest pathogens. The two primary factors leading to increased epidemic levels of Swiss needle cast appear to be warmer coastal temperatures within the last 20 years, and a higher proportion of Douglas-fir being replanted in coastal fog-belt areas where the warmer-winter climates and higher than normal Douglas-fir density support growth of the fungus (Manter, Reeser and Stone 2003). Many of these coastal plantation zones (>80%) have been found to be areas where Sitka spruce and hemlock, or other species besides Douglas-fir, were the dominant species in past stands (Manter et al. 2003).

As economic and cultural reasons for clear-cutting, fire suppression, and replanting with economically valuable species grew throughout the Pacific Northwest, the resulting denser, less-diverse plantations led to very different ecosystems. Predator-prey relationships that traditionally kept many native pathogens in check were thrown off, while the more limited growing spaces for young trees encouraged increased energy expenditure for competition and lower energy use for defenses against pathogens (Ripley 2002). In the absence of most other forms of disturbance, disease becomes a more

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[14] Phytophagous refers to plant eating species.

important disturbance-factor within these forests, often killing different trees than a forester would choose to thin from the stand, bringing these fungi and insect species to be seen as pathogens rather than contributors to the ecosystem (Ripley 2002). Looking at these species as pests is just one way of understanding their effect on an ecosystem. As Hansen and Goheen (2000, page 516) write,

> Pathogens first evolved, however, free of human expectations in much more complex ecosystems, and the destruction and loss we ascribe to them today are just one interpretation of their successful evolutionary strategy. Tree pathogens are integral components of forest ecosystems around the world, altering forests in many ways, both subtle and profound.

While both native and non-native pathogens kill trees, the species most successful in the long term are those species of fungi and insects that do not destroy enough of their host species to compromise their own survival. They tend to undergo sudden population explosions and cause wide-spread damage as the exception rather than the rule. Meanwhile, introduced pathogens—such as sudden oak death, Port-Orford-cedar root disease, and white pine blister rust—spread quickly throughout plantations and native ecosystems, creating much more widespread damage in most areas they have reached. Non-native plant pathogens often escape traditional conditions and controls—such as natural predators, competitors, or climatic limitations—with which they evolved (Ripley 2002). Also, host species may be extremely vulnerable to toxins or feeding methods of particular pathogens that they have never encountered in their entire evolutionary history (Ripley 2002).

# DISCUSSION

This section discusses the influence of native, versus introduced, forest pathogens on forests of the Pacific Northwest, and particularly in southwest Oregon and northern California. What does it mean for a plant species or pathogen to be native to the Pacific Northwest? The relationships between native pathogens and their natural forest communities often include subtle, yet complex interactions. Should we take the responsibility of protecting native species from human-introduced diseases, and if so how, and when, should we do this? Given that humans most likely introduced the *Phytophthora lateralis* pathogen in the first place, would it be considered ethical to take over the selection process of these trees from nature?

## I. What Makes a Species Native? Biogeography of the Pacific Northwest

The "nativeness" of a species to a particular region in Oregon or California is relative. The forests of the Pacific Northwest as we think of them today constitute a very narrow window in time of the ecological and evolutionary history of the coast range. For a large portion of its history (as recently as 15,000 years ago), large portions of the lands covered by the current north American rain forests were covered by glaciers (Hebda and Whitlock 1997). These forests have been shaped both by climatic variations and disturbances. Their present biodiversity resembles not only a geologically unique ecosystem in space, but also in the history of ecological time (Hebda and Whitlock 1997).

Our definition of an ecosystem pertains to both biotic and abiotic characteristics of a region, implying that these physical and biological components have interacted over time to establish a unique and fairly stable association of species and intricate web of life

(Hebda and Whitlock 1997). In the short-term, this stable, or climax community, may be interrupted by disturbances such as fire, wind, or disease, but will, through succession, eventually return to its former "climax" state. However, in geological time, even ecosystems such as these are temporary, a product of past evolutionary strategies and basis for future evolution among random plant associations. For instance, before around 25,000 years ago, Oregon's central Coast Range was covered in "an open forest of western white pine, western hemlock, and fir…and included mountain hemlock, red alder, and Sitka alder, and possibly yellow-cedar. The assemblage has no modern analog" (Hebda and Whitlock 1997). The discussion of the significance of native and introduced species in southwest Oregon and northwest California would not be complete without a brief description of previous vegetation patterns of the region.

Before 25 million years ago, open pine, alder, and hemlock forests were common in the central Oregon coast range. Between 25 and 14 million years ago, the most recent glaciation period reached its height, cooling mid-latitude northern areas, forcing the jet-stream more southerly than its present-day path, sending winter storms farther south, and lowering the winter moisture of the southern rain forests near the coast (Hebda and Whitlock 1997). During this glacial period, the coniferous rain forests of previous non-glaciated times in southern coastal areas largely disappeared, to be replaced by park-like and non-forested areas (Hebda and Whitlock 1997). In central Oregon, open lodgepole pine, mountain hemlock, fir, and Engelmann spruce forests were common, as the ranges of more of the present-day high-elevation species reached farther coastward (Hebda and Whitlock 1997). Between 12,000 and 10,000 years ago, the central Oregon coast range was forested with hemlocks, lodgepole pine, fir, and perhaps Sitka spruce, occurring in a mixed forest of unlikely northern coastal high elevation species, and temperate forest species, creating a forest of which there are no large present-day equivalents (Hebda and Whitlock 1997).

The more recent vegetation patterns occurring between 10,000 and 7000 years ago follow climatic patterns where lower (than current) solar radiation during winter, higher summer solar radiation, and draught during the summer supported alder, Douglas-fir, and some surviving spruce and hemlock in the southern coastal forests (Hebda and Whitlock 1997). From 7000 to 4000 years ago, lower summer solar radiation led to a great increase in moisture, creating forest ecosystems more closely resembling those present today. As the climate changed from warmer and drier to moist and moderate, western redcedar and western hemlock increased in Oregon, with Douglas-fir and hemlock also becoming more common (Hebda and Whitlock 1997). In the coastal rain forests of 3000-2000 years ago, late-successional species increased in some parts of northern California (as well as Washington), implying continued cooling in these areas (Hebda and Whitlock 1997). Meanwhile, true fir and Douglas-fir expanded their ranges throughout the Oregon Coast Range, suggesting a drier climate.

While not a notable forest species in Hebda and Whitlock's study (1997), the ancestors of the Port-Orford-cedar species have been present throughout the area for a very long time. In the Pacific Northwest, fossil evidence from between fifty-million to ten-million years ago suggests that ancestors of the current species of *Chamaecyparis* grew among a variety of plant associations, at temperatures fairly consistent with those of the present range of the species today (Zobel 1998). They were found in areas where temperature fluctuations were mild and where consistently moist areas existed over long amounts of time (Zobel 1998). The Port-Orford-cedar is said to have been part of a once much more widely distributed population of *Chamaecyparis*, which was condensed to its present range (Jimerson 1999; FSEIS 2004). While it is not known exactly why the Port-Orford-cedar became limited to such a narrow present-day range (it is suspected that availability of year-round water is a significant factor), the more recent impacts of humans have dramatically affected the distribution of this and other Pacific northwest forest species.

The arrival of humans to this landscape, at least 10,000 years ago, left a relatively light impact on the region, at least compared to the changes occurring following arrival of European immigrants. While the First Peoples certainly depended on and extensively utilized trees (especially the western redcedar, *Thuja plicata*), they seem to have managed them in a relatively sustainable manner (Hebda and Whitlock 1997). As Hebda and Whitlock write (1997):

> When widespread logging occurred, early-successional red alder expanded dramatically…the resulting assemblage resembles the pollen signal of the Douglas-fir-alder biogeochron of the early Holocene [10,000 to 7000 years ago]. There is little similarity to late-Holocene rain forest assemblages and, by implication, the way the forests were utilized by First Peoples.

Thus, although the current forested ecosystems of the Pacific Northwest represent thousands of years of evolutionary and climatic changes, rather than one stable, climax-state community, they have been changed relatively rapidly and dramatically by the arrival of Europeans in the last two centuries. Human-introduced species and pathogens further have the potential to alter these ecosystems on a timescale much smaller than many of those previously recorded in the region.

Currently, the rate of exchange of species between continents is much higher than it has been in the past (Mooney and Cleland 1998). The number and quantity of species crossing traditional biogeographic barriers is suspected to be very great, even though relatively few actually survive and reproduce successfully in the foreign environments. In the last 500 years, invading species have become dominant species on an estimated 3% of non-glaciated areas of the earth's surface (Mooney and Cleland 1998). In addition to the number of invasive species being carried across borders, those species already established in regions often grow in numbers through subsequent introductions, sometimes becoming invasive at certain population levels even in areas where they were not previously a problem (Mooney and Cleland 1998).

Invasive species have had several affects on native ecosystems. While invading species often must adapt and evolve quickly to their new environments, even native species may be forced to undergo rapid evolution in order to deal with invading species (Mooney and Cleland 1998). Meanwhile, as global extinction rates rise to a level significantly higher than they have been for the most part during the last 65,000,000 years, biodiversity in many populations is decreasing (Mooney and Cleland 1998; Woodruff 1998). This lower diversity has been known to lead to lower resilience in many endemic ecosystems, especially in response to invaders. Ecosystems with lower biodiversity are often much more prone to pests, weeds, and diseases (Woodruff 1998), not only because predator-prey relationships may be decreased, but also because loss of species leaves less competition and more open niches for new species to fill. Although the native range of a species is relative to time, the current rate of spread of species into distant ecosystems is very high. These unprecedented rates of invasions instigated by humans have the potential to weaken ecosystems, further destroying biodiversity, especially when an ecosystem's existing levels of biodiversity are already low.

## II. Why Breed and Protect Port-Orford-Cedar?

*Phytophthora lateralis* has already reached approximately 12,850 acres of federal lands where Port-Orford-cedar is a prominent species within its native range (FSEIS 2004). Under current management practices, it is expected to reach a total of around 20,400 acres or 21% of the range within 100 years (FSEIS 2004). Although total acreage involved gives a good idea of the extent to which this exotic pathogen has already spread, it is somewhat misleading because of the fact that higher concentrations of cedar sometimes occur on narrow strips of ultramafic soils near streams, swamps, and other water sources. These areas may represent a lower portion of total Port-Orford-cedar acreage, while also being sites where loss of the cedar will have the greatest environmental impact.

Protecting the remaining old-growth Port-Orford-cedar habitat is important, because once the pathogen is introduced into these areas it is unlikely ever to be eradicated. Instead, *Phytophthora lateralis* is likely to remain in the soil and within the infected watershed, colonizing the roots of Port-Orford-cedar seedlings and young regenerating stands, and killing most trees before they are able to reach a significant age anywhere near that of the ancient 300-400 year old stands (FSEIS 2004; Ullian and Jules 2000). Many of the remaining Port-Orford-cedar stands where the species is common are within late-successional and riparian reserves, where its ecological values are of great importance (Goheen 2000). Losing the species in these areas would mean losing a significant cover species—especially in the ultramafic soils where Port-Orford-cedar is one of the few canopy species. This would degrade ecosystems on which old-growth species preferring these late-successional characteristics depend (Goheen 2000). The Port-Orford-cedar's role in riparian areas as cover, canopy, shade, bank stability, and long-lasting downed woody debris is valuable regardless of soil characteristics (Ullian and Jules 2000; Goheen 2000). As Ullian and Jules (2000) write,

> The elegant adaptations of Port-Orford-cedar (POC) to riparian and wetland environments in southwestern Oregon and northern California make it an ecologically important component of these critical habitats…Observations thus far suggest that the role of POC is irreplaceable in many habitats. POC in riparian areas helps to shade streams, and to stabilize their banks, during high winter flows. At the end of its long life, fallen onto floodplain surfaces or in the streams it once shaded, POC's large trunk with its decay-resistant wood provides long-lasting and diverse habitat for salmonid fish and other aquatic life. As well, POC can act as an important channel-forming agent when it interacts with the stream.

The Port-Orford-cedar contributes to the aquatic habitats of several steelhead and coho salmon runs, including those of the Winchuck River, home to healthy steelhead stocks; as well as the Rogue, Chetco, Pistol, and Illinois rivers, several of which contain depressed winter or summer runs (FSEIS 2004). Nearly 2200 miles of Oregon streams in the range of Port-Orford-cedar support winter and summer steelhead habitat, although only around 301 of these miles were found to have Port-Orford-cedar immediately present (FSEIS 2004).

In addition to its role in aquatic and late-successional ecosystems, Port-Orford-cedar is part of many unique and rare plant-associations, in which it contributes biodiversity as well as often being one of the few—or only—canopy species (Ullian and Jules 2000). It is not known how or whether these species will be affected by its loss (FSEIS 2004). Port-Orford-cedar has been an especially important canopy species in riparian areas on serpentine soils. 10 % of the Port-Orford-cedar's northern range consists of ultramafic ecosystems, while 75% and 76% of the mid- and southern-range of the tree, respectively, consist of ultramafics (FSEIS 2004).

Preventive measures, especially washing muddy boots and vehicles to avoid tracking any outside mud or dirt into uninfected locations, as well as road closures during the wet season, are the most immediate way of protecting most uninfected areas. Once the pathogen has been introduced into a watershed, most Port-Orford-cedar associated closely with riparian areas will be lost, leaving a large age gap, even if resistant trees are planted in these areas. However, there is hope that replanting infected areas with resistant trees will restore these areas in the long term (FSEIS 2004). Disease-resistant Port-Orford-cedar planted in the most important high-risk sites—especially those areas where this species provides the main stream cover necessary for controlling water temperature—might compensate for at least 50 % of the environmental losses attributed to *Phytophthora lateralis* (FSEIS 2004).

There are several reasons for breeding Port-Orford-cedar for *Phytophthora lateralis* resistance. If the root-disease were not a problem, Port-Orford-cedar could be a very useful species in replanting cleared areas. In replanting efforts, it would create more diversity among the valuable timber species within plantations. Its economic value in replanting efforts is not limited to eventual lumber prices, since the diversity it creates within stands may help lessen the effects of other forest pathogens, as well (FSEIS 2004). Port-Orford-cedar is resistant to many of the native forest pathogens—such as laminated root rot and Swiss needle cast, and may also be resistant to other introduced pathogens, such as sudden oak death, *Phytophthora ramorum* (FSEIS 2004). It can grow in a broad variety of climates and conditions, as shown by its ornamental varieties that have been planted all over the world. Its ability to grow under very wet conditions is also valuable (FSEIS 2004).

In both ultramafic and other soil types, no other native species truly exhibits the characteristics of the Port-Orford-cedar which make it unique within its varying ecosystems. *Phytophthora lateralis* has influenced many forest stand structures—especially streamside cover—by killing all of the larger Port-Orford-cedar and by preventing the young trees from regenerating (Goheen 2000). The importance of streamside cover could be easily overlooked, yet its importance in maintaining fisheries, aquatic communities, and in preventing flooding is very great—not only in natural ecosystems, but for the support of human communities as well. The economic value of this species is also unique. During the height of harvesting and exporting Port-Orford-cedar, more than 40 million board feet were sold per year, a thousand board feet selling for as much as $6,000 (Hansen et al. 2000). Even though many closely—as well as more distantly—related species have similar wood qualities and characteristics, most do not grow as well or prolifically in the southern Oregon and northwestern California regions. The cultural value of this species remains significant to many people, while its aesthetic values as an ornamental species continue to be appreciated.

## III. Why biologists do not expect (or even attempt) to produce trees that are completely immune to mortality caused by the root-fungus.

Port-Orford-cedar will probably never be in danger of extinction due to the root rot, because they are prolific producers of seeds at an early age (FSEIS 2004). However, old-growth trees on poorly-drained sites whose roots are below the water-table remain at great risk, as up to 80 % of them (DSEIS 2003) are likely to succumb to the root rot over the next hundred years. Resistant trees being bred at the Dorena Genetic Research Center might eventually help replace even the older Port-Orford-cedar populations on sites that have already been infested. Meanwhile, specific genetic basis for resistance to the pathogen has not been found (McWilliams 2000), and so scientists are somewhat hesitant to replant areas with resistant trees before they understand more about what makes a tree resistant to *Phytophthora lateralis*.

Rather than trying to select trees for complete resistance to the fungus, biologists at Dorena Genetic Resource Center hope to establish populations that can survive in the presence of the fungus, since it is not likely to go away and since complete resistance may be nearly impossible. While even relatively resistant trees may succumb to the pathogen when subjected to very high inoculum loads, some of these trees may still reach much older ages than the very vulnerable naturally regenerating seedlings on infected soils. Thus far, even long-term stability of the resistant stock is not known, since trees bred for resistance have been exposed to the pathogen for only 16 years at most (FSEIS 2004). It is hoped, however, in breeding trees such as the Port-Orford-cedar and the white pine[15] for resistance, that the resistant trees and their pathogens will survive in relationships more similar to most native pathogens and their host species. As long as the

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[15] Since the 1950's, the USDA Forest Service has been screening and selectively breeding western white pines to increase proportions of white pine blister rust resistant trees for use in replanting and reforestation efforts throughout the range.

pathogen can survive without killing too many of its host species, both the forest community and the pathogen itself might benefit.

## IV. What is natural? An ecological perspective towards native forest pathogens

Are high levels of pathogens "natural" for a forest? Should a forest be considered "healthy" when many diseases exist? When and where should humans decide to intervene or manage the forests? Most forest pathogens have traditionally (at least in the last two centuries of western American forestry) been seen as pests, as foresters assumed a park-like model as "normal" or ideal for American forests. As Hansen and Goheen (2000) write:

> Our views of forest pathogens are inevitably dominated by a few exotic pathogens in vulnerable forests and a strong professional legacy—the idea that a goal of forest management is regulated, disease- and decay-free trees on the nineteenth-century European model (Meinicke 1916). Even today, there is little appreciation for the significant effects that indigenous pathogens have on natural forests.

Part of this view of pathogens as "unnatural" stems from a misunderstanding about the roles many of these tiny forest species play in their ecosystem. Secondly, in an attempt to gain the most profitable lumber in the shortest amount of time, pathogens are seen as a hindrance rather than a viable component of tree plantations and older forests alike (Ripley 2002). Similar beliefs having to do with fire further eliminated an important disturbance factor from many forest ecosystems.

A fuller, more ecological approach can be taken that recognizes the forest ecosystem as a dynamic system where plants are only some of the many inhabitants and where disturbance is important in creating and maintaining diversity and structure. This section will look at forests from this point of view, asking what human roles contribute to continuing and encouraging this dynamic system. From this perspective, exotic pathogens still differ in their relationship and impact—not only on individual trees—but on the forest ecosystem as a whole.

Although woody plants and charismatic mammalian species are perhaps the most easily recognizable and well-known forest species, they are part of, and depend upon, a much more complex web of life. In most northwest forests, bacteria, fungi, insects, and other arthropods account for a high amount of the overall biodiversity, constitute a significant amount of the below-ground forest biomass, vary greatly in population sizes in short amounts of time, and impact (or even control) many ecosystem functions (Schowalter et al. 1997). Insects and fungi often have incredible reproductive potentials—with the capability of producing somewhere between hundreds and millions of offspring in as little as two weeks' time (Schowalter et al. 1997), allowing them to disperse and evolve rapidly when the opportunity arises. Because of this awesome evolutionary potential, any given location may become home to hundreds of species of fungi and insects, some not yet even named or described (Schowalter et al. 1997).

In Douglas-fir dominated forests of western America, 439 species of fungi have been found (Hansen and Goheen 2000). Root rots, heart-rots, and stem-decaying fungi become important components in old-growth forests, slowly decaying vulnerable trees. Canker-rots invade cambium and kill both the sapwood and heartwood, while decay fungi infect fire-scars and wounds, and stem-decay fungi—often in association with termites and ants—also colonize trees. These fungi contribute to species diversity, create snags, add to the accumulation of woody debris, and help form multi-layered canopies of diverse ages and species (Hansen and Goheen 2000). The resulting large chunks of dead and downed wood are colonized by numerous fungal species, followed by vast galleries of insects. Woodpeckers and other birds feed on the insects, while other small mammal and bird species eventually move into the cavities they create. Eventually, decayed wood contributes to the rich layer of humus on the forest floor, supporting more plant life. Thus, rates of decomposition, nitrogen, and carbon cycles are often sped up by these processes, as well.

Although most tree species are resistant to attack by the majority of bacteria, fungi, insects, and other arthropods within their ecosystem, phytophagous insects and fungal forest pathogens have usually evolved in close association with host species (Ripley 2002), finding ways to overcome host-species resistance strategies (Schowalter et al. 1997). Nearly all have strong preferences for a particular (or several similar) host species (Wilhite 2002; Schowalter et al. 2002). They have evolved many different specialized strategies for obtaining their energy from live trees. They range from more or less mildly parasitic relationships to instigators of deadly diseases (Schowalter et al. 2002). Some, such as bark beetles and canker fungi, as well as many of those species discussed above, attack weak and dying trees, weeding out the most vulnerable species in a stand (Schowalter et al. 1997), and feeding mainly on dead or dying plant tissues. Others—root fungi, rust fungi, and insects such as aphids—require live, healthy trees, usually dying when their host plant dies (Schowalter et al. 1997). Many of these species prefer needles and leaves, rarely killing the entire plant, except in extreme conditions or during years when their population size is very large. These species also alter forest communities by influencing energy and nutrient cycles, as well as by changing the competitive or reproductive success of species. Still other species of plant pathogens kill the tree or even groups of trees, affecting the forest structure on a much larger scale (Hansen and Goheen 2000). These species—such as beetles, decay fungi, and the laminated root rot (*Phellinus weirii*) influence forest communities by altering the local structure and population composition, as well as affecting landscape-level diversity and succession stages within a forest. Structurally, these latter types (pathogenic species) change stand composition in one of two ways. They often either kill nearly all (including the larger, more successful) living members of their host species that they encounter—opening up canopy space for younger trees, or they kill only smaller, younger, and more vulnerable trees—helping maintain larger, healthier trees within a stand (Schowalter et al. 1997).

As one of the most fascinating of these wide-spreading endemic forest pathogens, the Douglas-fir form of laminated root rot is interesting in that it infects and kills large patches of dominant coniferous species. As such, its focus on a few specific species is actually important in creating more biodiversity within several types of coniferous forests. For instance, in many west-side forests, mortality centers caused by laminated root rot regenerate with disease-resistant trees. In higher elevations of the Cascades, gaps in late-successional western hemlock created by the root rot are often filled in with earlier successional species—especially rot-resistant pines—increasing diversity and structure within stands (Hansen and Goheen 2000). Meanwhile, in old-growth Douglas-fir stands, later-successional species—such as the highly shade-tolerant western hemlock and western redcedar—often colonize these patches. When clearings left by the laminated root rot fill with young vegetation, mammals, birds, and insects may move in, feeding off of the herbaceous and shrubby vegetation, and colonizing downed trees and snags (Schowalter et al. 1997; Hansen and Goheen 2000).

Many species of fungi and insects kill individual trees, often working together or in close succession. Several rot-causing fungi greatly weaken, and sometimes kill trees. The brown cubical butt rot and red ring-rot fungi are some of the primary fungi responsible for killing single trees in older Douglas-fir stands. Both fungi kill trees, although red ring-rot often weakens trees to the extent that the Douglas-fir beetle can colonize them, so that it is difficult to attribute the cause of death to just one of the pathogens (Schowalter et al. 1997). Other insects—such as mountain pine beetles, western pine beetles, and southern pine beetles—sometimes act as highly destructive pathogens, attacking all pines within denser stands of a particular size class or weakened state, and altering them within several years (Schowalter et al. 1997). Infestations such as these either create stands composed of more non-host species, or encourage stand-replacing fires that clear the way for a new stand of pine.

Insects and fungi acting as pathogens are most striking in forest ecosystems when they kill trees. As with other disturbances—fire, flood, storms, and logging—these events determine the characteristics of a stand, creating a uniqueness that parallels the uniqueness of the individual disturbance-causing fungi and insect species within the stand. In those ecosystems where other disturbances—such as fires—are relatively infrequent, disease-causing species bring about the most influential disturbances (Schowalter et al. 1997; Hansen and Goheen 2000). One of the interesting things about forest life is the way it is connected to forest death. Through dying, the opportunity for more life is created, new niches become available, more biomass is brought to the forest floor, and pieces of the canopy are opened up. Often, within these ecosystems, life becomes defined through the way it is destroyed.

One of the main differences between native and non-native forest pathogens often has to do with the speed in which the pathogen spreads through a stand, rather than just the extent of mortality the pathogen causes in a particular area. Exotic pathogens—since they are usually separated from most of their native, natural prey species, predators, and limits on their population size or speed of dispersal—often spread relatively rapidly throughout a foreign ecosystem (Ripley 2002). While most introduced species fail to establish in an ecosystem, of the few that characteristically grow and reproduce successfully, usually only around 1 % of these species (Mooney and Cleland 1998) will become invasive or pathogenic in their new environment. However, the relatively few introduced species that both establish and become invasive are often responsible for causing widespread damage or mortality among host species or the host community.

While some native pathogens—such as the laminated root rot—also kill most host species they come into contact with, they tend to move much more slowly. The speed with which the exotic pathogen is able to spread often exceeds ecosystem limits, wiping out, rather than thinning out, particular species. Unlike native pathogens, which have evolved with and depend on the continued success of their host species, introduced pathogens do not characteristically share this trait (Hansen and Goheen 2000). This is the case with *Phytophthora lateralis*, which has spread so rapidly throughout the Port-Orford-cedar range that the ecosystem may not have much time to compensate for loss of this tree species. Several introduced species have similarly affected forests of the Eastern United states, including *Phytophthora cinnamomi* root disease, chestnut blight

(*Cryphonectria parasitica*), and Dutch elm disease (*Ophiostoma novo-ulmi*). Sudden oak death, *Phytophthora ramorum*, also threatens to do this, although perhaps on a much greater scale, since it infects a wide variety of trees that have much more wide-spread ranges.

## VI. Our Responsibilities towards Protecting Native Species from Human-Introduced Diseases.

It would be difficult to argue that *Phytophthora lateralis* was not introduced by humans, given the location of first diseased trees and the world-wide trade in ornamental cultivars of the host species at the time the pathogen began killing Port-Orford-cedar. However, even if we did conclude that the pathogen was dormant in forest soils, or evolved within the range of Port-Orford-cedar, the wideness and suddenness of spread would still need to be attributed primarily to humans. Since humans spread the pathogen throughout the Port-Orford-cedar's native range and across so many watersheds so efficiently, the amount of time the species had to become resistant to the pathogen was greatly diminished.

In attempts to breed more highly resistant varieties of Port-Orford-cedar, we are also speeding up another potentially thousand-year-long process. Although it is difficult to know how effective this method will be compared with natural selection, one might hope that it will make up for, in some part, the changes that the pathogen has brought about in the native ranges of the host species. By breeding resistant cedar, we might hope to reestablish the Port-Orford-cedar within its native range before the forest and stream structures change greatly in response to the loss of this species. Reintroducing more resistant cedar in aquatic areas where it has been wiped out will also help protect the aquatic habitats and their associated species that have lived and existed under the cover of Port-Orford-cedars and their ancestors for many thousands of years.

While other water-loving, coastally restricted *Chamaecyparis* species may resemble the Port-Orford-cedar in some respects, none of them would be as well adapted to the particular climate, elevation range, or soil conditions as the Port-Orford-cedar. Also, planting non-native trees in the Port-Orford-cedar's native range does little to preserve the endemic or native forest structure that has survived here for centuries. In a sense, planting foreign trees would also be introducing more species, along with any other plant pathogens that might be associated with their foreign soils. Even the decision to take no action towards this exotic pathogen would itself be an action (Schowalter 1997; Hansen and Goheen 2000), one that might have a much more negative impact on the existing ecosystems—as well as their abilities to evolve in the future.

## VII. The Ethics of Altering, or Even Taking Over, the Selection Process from "Nature."

Why breed resistant trees? What effects will these resistant trees have on the ecosystem, or on the future of their species? This question came up after introducing the subject to my Clark Honors College senior thesis seminar. Concerns relating to breeding trees include ecological issues, as well as genetic diversity and biodiversity issues. Will the resistant trees have identical biological needs as the cedars lost to root rot? Will they interact with other organisms—aside from the root rot—in similar ways? Will this form of resistance be permanent, or will the fungus overcome the Port-Orford-cedar's limited defenses? Will significant genetic diversity be lost by selecting only resistant trees from among the hundreds of potential parent trees? These questions relate to what we perceive as "naturally occurring," as well as how much we want to include in this debate the other influences of humans on these trees and their ecosystems over the last two hundred years.

One important consideration when selectively breeding smaller groups of individuals within a species for disease resistance is maintaining genetic diversity within the population. If a population of resistant Port-Orford-cedar is used to replant areas where *Phytophthora lateralis* has killed native trees, maintaining the genetic diversity within that population is important. Loss of genetic diversity may be effective in the short term as all (rather than just some) of the individuals are successful and may even excel at survival in current biological and environmental conditions. However, as changes over time develop in the ecosystem, climate, and biota, the species needs a diverse genetic background to draw from in order to continue producing a dynamic, adaptive population. It is believed that the Port-Orford-cedar has historically occupied a much greater area than its present distribution, reaching parts of Idaho and Montana, and even as far as Nebraska, around ten to fifty million years ago (A Range-Wide Assessment 2003, FSEIS 2004). From this larger geographical distribution the Port-Orford-cedar retained much of its past genetic diversity in the relatively small current range (FSEIS 2004). Genetic variation between trees within stands has been found to be high, so that even if some stands were completely lost, a great deal of genetic diversity would remain (FSEIS 2004). However, these genetic studies also found that Port-Orford-cedar possessed some rare alleles in individuals or stands at the edges of its range, which could potentially be lost.

While selective breeding has had a significant impact on many plant varieties (for example, wheat varieties bred during the green revolution became much shorter, more fruitful, and requiring of more direct attention through watering and fertilizer than their less intensely bred counterparts), it remains a process that is potentially present already in the natural genotypes of the species. Unlike gene splicing, selective breeding of root-disease-resistant Port-Orford-cedar relies on choosing those individuals already resistant, which could potentially breed with one another in natural ecosystems, and increasing their numbers in proportion to non-resistant species. This speeds up the process that could happen eventually in the native forests anyway, since once most of the susceptible Port-Orford-cedars have become infested with *Phytophthora lateralis*, the remaining individuals would be the only ones left to reproduce. Even though the specific factor responsible for *Phytophthora lateralis*-caused root disease has not been determined, very little variation has been found in the *Phytophthora lateralis* species itself. Therefore, the pathogen is not expected to evolve ways around the resistant plants' defenses.

Breeding Port-Orford-cedar for resistance to *Phytophthora lateralis* may not be effective in the short run, since many of the ecosystem (as well as economic and aesthetic) needs served by the Port-Orford-cedar are accomplished by much older trees. However, the resistance-breeding program does offer an excellent opportunity to develop resistant seedlings that can be used to re-seed many infested watersheds. While the Port-Orford-cedar breeding program is partially focused on bringing back a valuable timber species, and is funded in part by an economic-driven desire, ecological values also play a role in reasons for breeding root-rot resistant trees. Root-disease-resistant trees should eventually be ecologically helpful throughout their native range, supporting aquatic habitats and contributing to the diversity of canopy species in plantations, as well as in mature and old-growth stands.

## CONCLUSION

The Port-Orford-cedar is a unique tree species whose loss will impact ecosystems, though probably not so severely as to prevent any ecosystem from functioning without it. While breeding for resistance seems to be a fairly successful, straightforward, and helpful approach, prevention of further disease spread into uninfested areas is still the most effective strategy for protecting many ecosystems. The current Port-Orford-cedar resistance breeding program has followed traditional horticultural selection techniques which imitate natural selection and select parent trees from geographically relevant seed sources. In addition, the genetic variation within families is often very high, perhaps greater than that among separate stands, increasing the potential for diversity in resistant stock even from a few families. Significant genetic diversity is not likely to be lost in breeding resistant individuals, while the ethics of breeding these trees are not much more controversial than those related to raising most native tree species in nurseries for reforestation efforts. The preventive and remedial efforts to turn around the destruction humans have brought to this species through introduction of the pathogen dims in comparison to the rate of spread, establishment, habitat alteration, and extinction which the human species is causing around the world. Breeding resistant trees offers some hope in a frustrating struggle to compensate for unexpected consequences to peoples' desire for ornamental and exotic horticultural varieties.

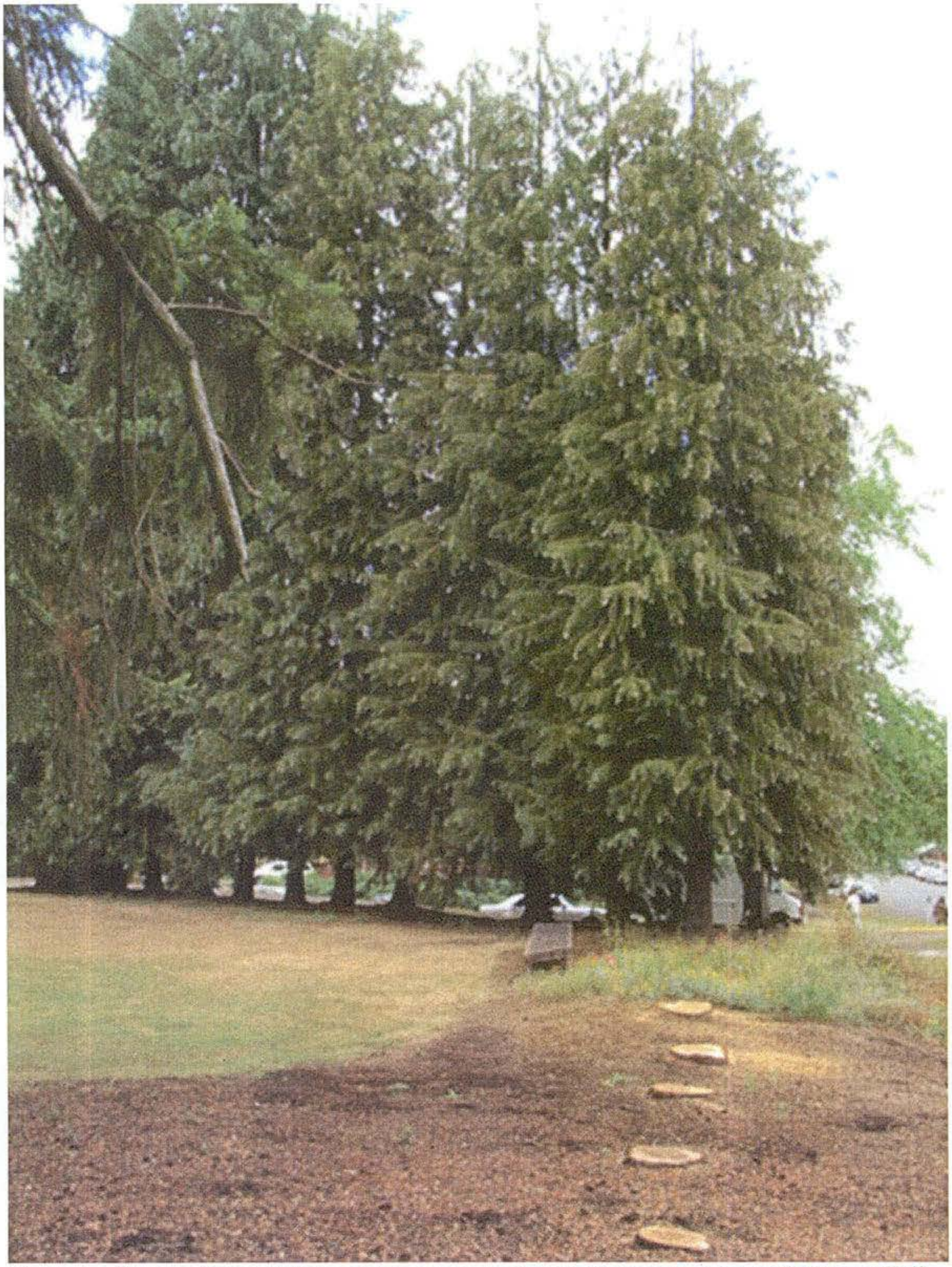
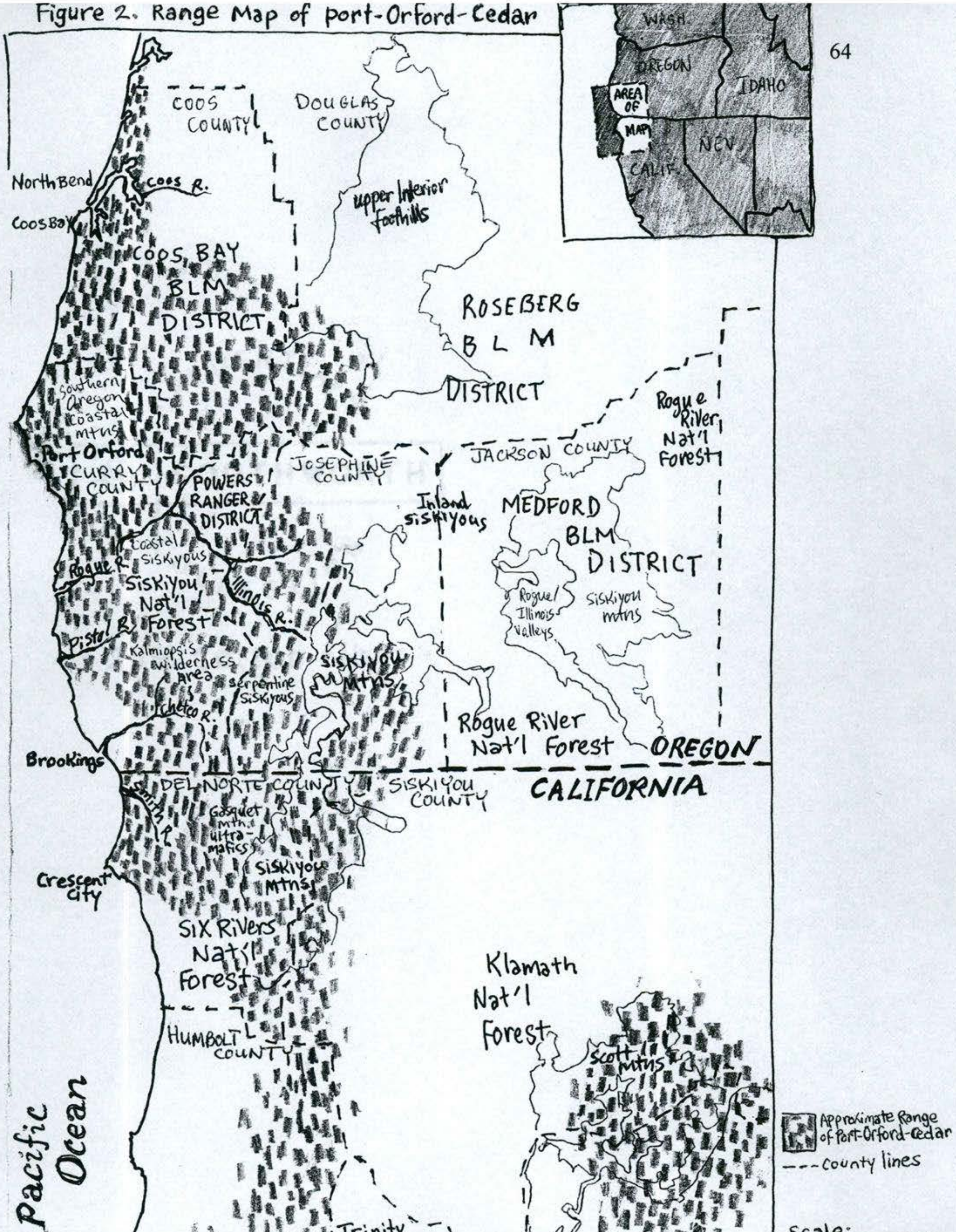


Figure 1. Grove of Port-Orford-cedar, *Chamaecyparis lawsoniana*, near Gerlinger Hall and University Street. University of Oregon Campus, Summer 2004.

Figure 2. Range Map of Port-Orford-Cedar



Sources: Port-Orford-cedar SEIS (2004), National Forest Service Website (www.na.fs.fed.us), and Oregon Dept. of Forestry (www.odf.state.or.us).

Figure 3. "Berry-like" cones and sprays of foliage on Port-Orford-cedar (*Chamaecyparis lawsoniana)* near Gerlinger Hall, University of Oregon Campus. Photos taken July 19, 2004.

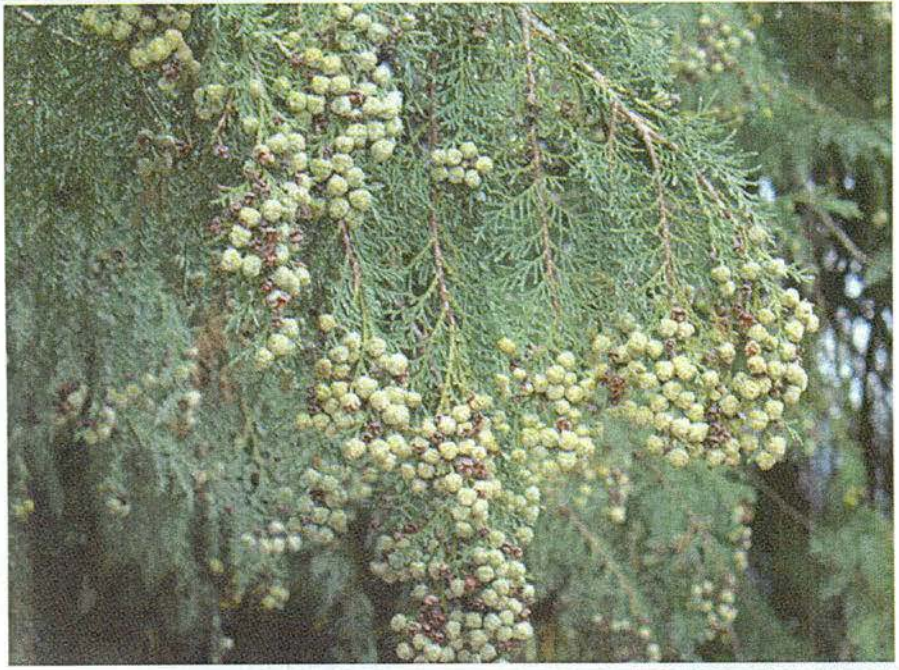


Figure 4. Dying Port-Orford-cedar (*Chamaecyparis lawsoniana*) near Fenton Hall, University of Oregon Campus. Photo taken in late July, 2004.

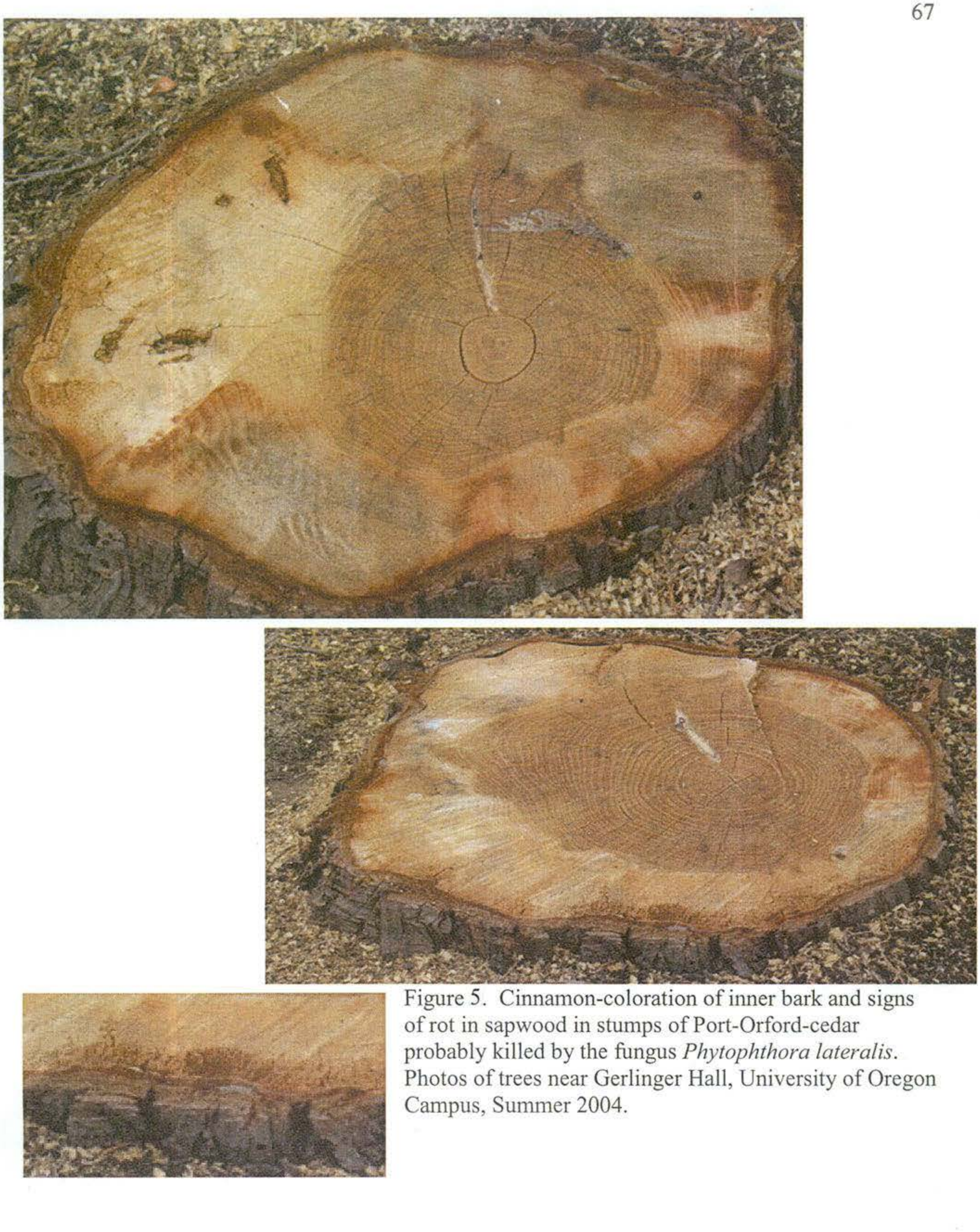


Figure 5. Cinnamon-coloration of inner bark and signs of rot in sapwood in stumps of Port-Orford-cedar probably killed by the fungus *Phytophthora lateralis*. Photos of trees near Gerlinger Hall, University of Oregon Campus, Summer 2004.

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