

Chapter 3

Phytophthora lateralis and Other Agents that Damage Port-Orford-Cedar

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Introduction

Port-Orford-cedar root disease is caused by the pathogen *Phytophthora lateralis*. The name *Phytophthora* means “plant destroyer,” and the genus contains many destructive plant pathogens that are distributed throughout the world. Plant diseases often are most damaging when non-native pathogens are introduced into new areas. The Irish potato famine of the 1840s caused by *P. infestans* (Mont.) de Barry and the current mortality of a large number of plant species in Australia due to *P. cinnamomi* Rands, provide graphic examples of the destruction that introduced *Phytophthora* species can cause. Although the origin of *P. lateralis* is unknown, it is likely that the current mortality of Port-Orford-cedar is another example of damage due to such an introduction.

Many investigators believe that *P. lateralis* is an Asian species (Tucker and Milbrath 1942, Zobel et al. 1985) although the pathogen has not been found in Asia. Europe has been suggested as another possible point of origin (Erwin and Ribeiro 1996) and investigators have confirmed the identity of *P. lateralis* isolated from container-grown Port-Orford-cedar seedlings in France. However, it is strongly believed that its presence there resulted from a recent introduction from North America rather than a natural occurrence (Hansen et al. 1999). Another theory is that *P. lateralis* may have originated from some location in North America outside the native range of Port-Orford-cedar, possibly on yellow cedar (*Chamaecyparis nootkatensis* [Lam.] Sudw.)¹. However, infected yellow cedars have only been observed under laboratory conditions (Torgeson et al. 1954) and when the species was planted with Port-Orford-cedar on heavily infested experimental sites (McWilliams 2000a). They have not been found in natural stands.

P. lateralis has a narrow host range. Besides Port-Orford-cedar, only Pacific yew (*Taxus brevifolia*) has been reported to be infected in the wild (DeNitto and Kliejunas 1991, Kliejunas 1994). Pacific yew is much less susceptible to the pathogen than Port-Orford-cedar, and evidence indicates that it mainly becomes infected when in close association with many already-infected cedars (Murray and Hansen 1997). Outside of the native range of Port-Orford-cedar, *P. lateralis* has been identified on ornamental Port-Orford-cedar in British Columbia, Washington, Oregon and northern California. The pathogen has also been reported in other states, as well as other countries, including New Zealand, Germany and France. It has been confirmed only in France (Hansen et al. 1999).

Taxonomy

P. lateralis is an Oomycete belonging to the family Pythiaceae. Formerly considered to be true fungi, it is now known that Oomycetes are quite different. Although they are somewhat fungus-like, Oomycetes are more closely related to biflagellate algae than to fungi (Beakes 1987, Dick 1982). It is now generally accepted that Oomycetes constitute a separate kingdom from the fungi (Cavalier-Smith 1986, Dick 1995, Erwin and Ribeiro 1996, Parker 1982).

Life Cycle

All *Phytophthoras* exist primarily as hyphae, or thin threads of fungus-like material adjacent to and within their host. Aggregations of hyphae are known as mycelia. Mycelia, if fragmented or transported along with pieces of host plant, can serve to move the pathogen to new locations. Mycelia are somewhat fragile and die when exposed to drying conditions. Several spore types form as specialized structures attached to *Phytophthora* mycelia.

¹Roth, L.F.; Goheen, D.J. 1977. Personal communication. Roth, retired, Plant Pathologist, Oregon State University. Goheen, Pathologist, USDA

Most *Phytophthoras* have four spore types, with different environmental tolerances and functions: zoosporangia, zoospores, chlamydospores, and oospores (fig. 3.1). Zoosporangia (often simply called sporangia) are thin-walled sacs that form at the ends of mycelial branches. In some species, these sporangia can break off (caducous sporangia) and be readily spread overland by water or wind to infect new hosts. Although there are reports of *P. lateralis* infecting Port-Orford-cedar foliage via rain splash on rare occasions (Roth et al. 1957), there appears to be little evidence that the pathogen produces caducous sporangia in nature. Caducous sporangia are produced by *P. lateralis* in culture under some conditions, but the significance of this for field situations is unclear.²

Sporangia can also remain attached to the original mycelium and the contents can differentiate into zoospores. When mature, and generally in the presence of free water, the zoospores are released (fig. 3.2). Zoospores lack cell walls, are very delicate and have two flagella. They can swim for several hours before forming cysts, but can only travel an inch or two in standing water (Carlile 1983). Zoospores also have the ability to detect compounds released by a host and swim in the direction of the host. Upon contact with a host rootlet, the zoospore will attach itself and germinate. If a host rootlet is not found, other surfaces are contacted, or agitation occurs, a zoospore will form a cyst. When encysted, it can be carried considerable distances in running water. In contact with a host, the cyst can germinate and form a mycelium that infects the host, or it can form another sporangium and release more zoospores. Infection by sporangia and zoospores of *P. lateralis* occurs primarily through the succulent growing tips of small Port-Orford-cedar rootlets that occur in the duff or at shallow depths in soil. Port-Orford-cedar produces a multitude of fine rootlets in these strata (Gordon and Roth 1976, Zobel



Figure 3.1—Spore types of *Phytophthora lateralis*

² Hansen, E.M. 1998. Personal communication. Professor of Forest Pathology, Oregon State University, Department of Botany and Plant Pathology, Corvallis, OR.

et al. 1985). Sporangial development and zoospore production are favored by cool, moist conditions and are optimal at temperatures between 50° F and 68° F (Trione 1974). Under favorable cool, wet conditions, *P. lateralis* populations can increase rapidly in areas where hosts are numerous because of the rapid and continuing production of flagellate zoospores and other spore types.

Chlamydospores are thick-walled vegetative spores (fig. 3.1). In *P. lateralis* cultures, they form abundantly and are laterally attached to the mycelium. Chlamydospores are more resistant to drying and temperature extremes than mycelia or sporangia. They can germinate directly and form infective mycelia or, in the presence of water, they can form sporangia and release zoospores. Ostrofsky et al. (1977) showed that, under laboratory conditions, *P. lateralis* populations detected by baiting³ decreased substantially when unfavorably warm, dry conditions typical of summer months in the range of Port-Orford-cedar occurred. However, the pathogen survived at a reduced level as chlamydospores in organic matter, especially in small roots on infected trees and fragments of roots in the surrounding soil. Hansen and Hamm (1996) have demonstrated that *P. lateralis* can survive in infected Port-Orford-cedar roots and root fragments for at least seven years under favorable conditions. *P. lateralis* chlamydospores are incapable of direct movement, but their structure provides protection during passive movement in infected roots or organic material in soil and mud.

The fourth spore type produced by *Phytophthora* species is the oospore, which is a sexual spore. *P. lateralis* is homothallic, meaning a mycelium resulting from a single zoospore can form oospores without another mating type being present. The oospore is the spore stage most resistant to drying and environmental extremes, and can survive for many years before germinating. As with the other spore stages, an oospore can germinate

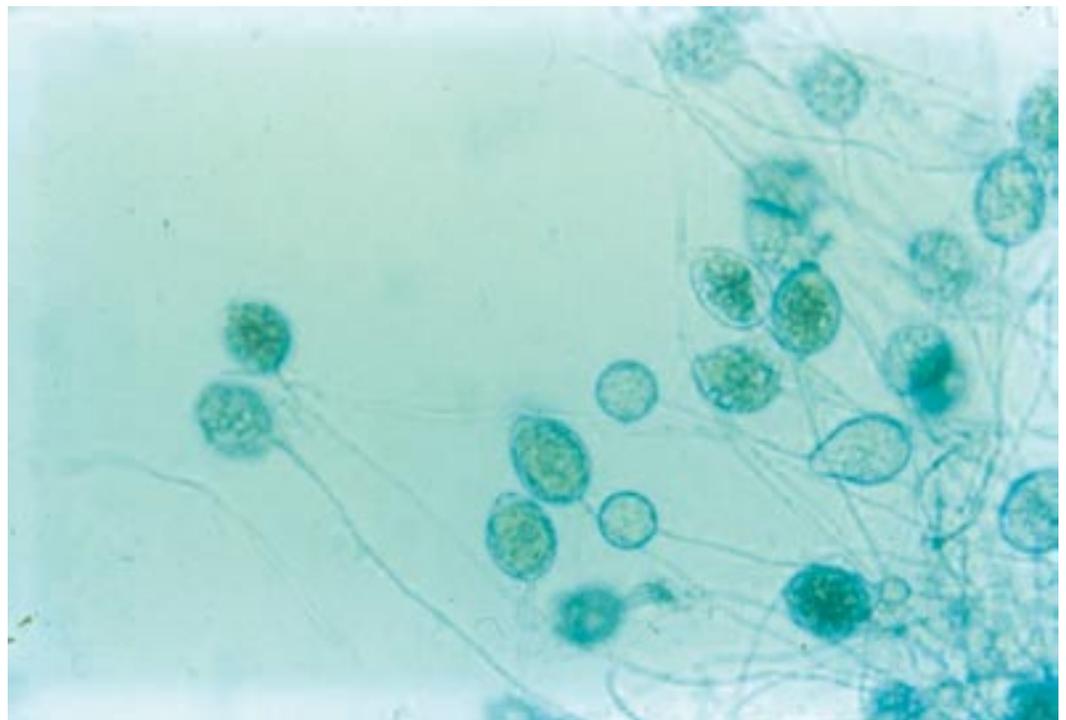


Figure 3.2—*Phytophthora* sporangia containing zoospores

³ Baiting is a type of bio-assay that uses Port-Orford-cedar seedlings to determine the presence of *Phytophthora lateralis*. Non-resistant Port-Orford-cedar seedlings are planted in soil or placed in streams where *P. lateralis* is suspected to occur. After an exposure period of four to eight weeks, the seedlings are recollected and examined for cambial stain, a diagnostic symptom of infection by *P. lateralis*. To confirm the diagnosis, root tissue from a subsample of seedlings is cultured on a selective media and examined under a microscope for the sporangia characteristic of *P. lateralis*.

directly to form a mycelium, or produce sporangia and zoospores. Oospores are rarely seen in cultures of *P. lateralis* unless a special medium is used, and their importance in the life cycle of this species in the forest is unknown.

Mode of Transport

Long distance spread of *P. lateralis* results from moving infected seedlings or infested soil into previously disease-free sites. Humans have been the primary vectors of the pathogen. Major spread in forests has occurred via earth movement in road construction, road maintenance, mining, logging, and traffic flow on forest roads (Kliejunas 1994, Roth et al. 1957, Roth et al. 1972) (fig. 3.3). In general, the pathogen has not spread into areas where a lack of access has prevented human activity. Movement of the pathogen in organic matter in soil clinging to the feet of elk, cattle, and humans also is known to occur but on a much more localized basis than that associated with vehicles (Harvey et al. 1985, Kliejunas 1994, Kliejunas and Adams 1980, Roth et al. 1972). Spread of *P. lateralis* occurs primarily in the late fall, winter, and early spring when the cool, moist environmental conditions favorable for the pathogen prevail. Unless there are unusually wet conditions, little or no spread occurs in the hot, dry summer months.

Once infested soil is deposited along a road or trail, *P. lateralis* can travel down slope in water. In order to facilitate further spread, this relatively small amount of inoculum must encounter a new Port-Orford-cedar host in the immediate area. Port-Orford-cedar is not usually infected more than 40 feet downslope from roads or trails, except where streams, culverts, wet areas or other roads are present to facilitate further dispersal (Goheen et



al. 1986). Infection of a new host in the immediate vicinity of the road or trailside results in the production of numerous additional zoospores and chlamydospores, increasing the likelihood of further downslope disease spread (Goheen et al. 1986, Hansen 1993). Preliminary study results show that Port-Orford-cedar can be infected at least 164 feet down a stream below a road crossing (Jules and Kauffman, 1999). Anecdotal evidence implies that disease spread may be much further.

While swimming zoospores may travel downstream in freely moving water, spread of the disease over longer distances is most likely accomplished by the more resilient chlamydospores and encysted zoospores. If by chance these spores encounter

Figure 3.3—Favorable conditions for spreading *Phytophthora lateralis* by vehicles

a new Port-Orford-cedar host, they may germinate and form mycelium that initiates infection. Alternately, chlamydospores and encysted zoospores may germinate to produce additional sporangia and swimming zoospores. If released near a new host, these zoospores may swim the remaining short distance to initiate infection.

In virtually all cases, infection of Port-Orford-cedar by *P. lateralis* occurs in areas where obvious avenues for water-borne spore dispersal exist. Infection is dependent on the presence of free water in the immediate vicinity of susceptible tree roots (figure 3.4). High risk areas for infestation include stream courses, drainages, low lying areas downslope from existing centers of infestation, and areas below roads and trails where inoculum is introduced. The position of previously disease-killed cedars along the length of the stream channel is not necessarily a good predictor of the sequence of infection, as trees upstream are not always infected earlier than those located further downstream. However, it has been found that trees nearer to the center of the stream channel become infected earlier than those growing farther away from the stream (Kaufmann and Jules 1999). The spread of disease within a stream appears to follow a classic epidemic pattern, with levels low in the first years, increasing to a maximum number of new infections, and then decreasing again in subsequent years (Kaufmann and Jules 1999).

Topography has a considerable influence on the spread of the pathogen. Steep slopes, dissected by drainages, can quickly channel infested water into streams whereas cross slope spread is more restricted. On broad slopes or flat areas, infested water may spread out over larger areas and move more slowly. Because they are easily flooded, concave areas with Port-Orford-cedar are very vulnerable to infestation. Cedar on convex slopes, on the other hand, exhibits limited vulnerability. Port-Orford-cedar growing on sites or micro sites that are unfavorable for spread of the pathogen often escape infection, even in areas where infected trees are nearby. Tree-to-tree spread of *P. lateralis* via mycelial growth across root contact does occur (Gordon and Roth 1976) but is considered to be much less significant in the epidemiology of the pathogen than spread by spores in free water.

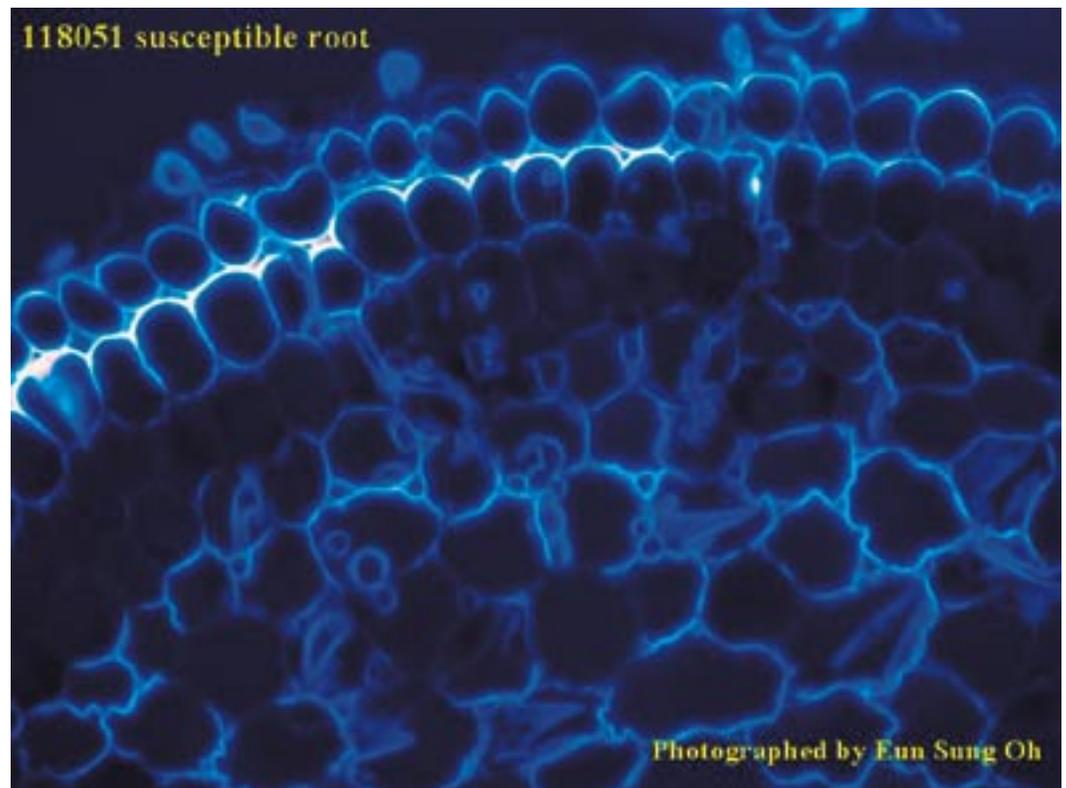


Figure 3.4—*P. lateralis* infected root

Genetic Variation

Relatively few studies have focused on the genetics of *P. lateralis*; however, the question of variation in isolates of the pathogen is an important one. It is necessary to know the range of variability in pathogenicity and virulence among isolates so that appropriate resistance can be incorporated into the ongoing Port-Orford-cedar breeding program. It is also necessary to know the variation in virulence so that appropriate isolates can be used in testing for resistance. The amount of genetic variation among isolates will offer important data for determining population structure of *P. lateralis* and whether the pathogen exhibits a simple structure compatible with the idea of introduction. If genetic information is consistent with the idea that this pathogen was introduced to North America, then it should support efforts to determine its origin, and give some basis for comparison if that location is ever found.

Some studies examining spore production, growth, lesion length produced on inoculated hosts, uniformity of isozyme profiles, and DNA fingerprinting have been conducted on *P. lateralis*. In a comparison of ten isolates from Oregon, nine isolates were found similar in sporangia production and all ten produced oospores equally well. The isolates, however, varied in chlamydospore production (Trione 1959). In 1991, a study of 11 isolates from Oregon and California showed identical isozyme banding patterns (Mills et al. 1991). A study in 1990 demonstrated the lack of variability among 23 isolates collected from throughout the range of Port-Orford-cedar (Hansen unpublished). Only one isolate grew more slowly than the others. There were significant, but unrepeatably, differences in zoospore production but no differences among total protein and isozyme bands. The one isolate that grew more slowly also caused significantly shorter lesions in inoculation tests. The authors suggest that a simple difference in growth rate could produce differences in zoospore production and pathogenicity. A recent study compared growth rates, virulence, and DNA fingerprints among 13 isolates of *P. lateralis* collected from Canada to California (McWilliams 2000a, b). Isolates were grown on two types of agar and were from three hosts: naturally infected Port-Orford-cedar and Pacific yew, and experimentally infected yellow cedar. To examine any differences in virulence, three inoculation methods were used. One method involved inserting a block of mycelium under the bark of rooted cuttings, a second method involved inoculating detached stems with zoospores, and a third method involved inoculating intact root systems with zoospores. Results showed some differences in growth rates but nearly identical DNA banding patterns. One isolate, of the 13 used, produced significantly shorter lesions in the inoculation experiment. There were no differences in the lesion lengths of other isolates.

The near uniformity of DNA fingerprints and isozyme profiles in the studies previously described suggests limited genetic variability in the *P. lateralis* found in the native range of Port-Orford-cedar. The genetic uniformity found in *P. lateralis*, combined with the extreme susceptibility of the host, provides evidence that this pathogen was probably introduced into the Port-Orford-cedar native range. Given the genetic uniformity of this pathogen, it is interesting to note the significant difference in virulence found in one isolate in the 2000 study. This difference may be due to diminished virulence attributable to lengthy storage conditions or other factors. The differences in lesion length when roots and shoots are exposed to zoospore inoculum may be due to differences in the susceptibility of roots and stems, differences in host mechanisms to limit growth in the different plant tissues, or because of variations in the inoculation technique or number of zoospores in the inoculum.

The lack of genetic variability in *P. lateralis* suggests that if Port-Orford-cedar trees resistant to the pathogen can be found or developed through a breeding program, the resistance should have a strong likelihood of persisting over time.

There remain unanswered questions about the biology and epidemiology of *P. lateralis*. The role of the occasionally caducous sporangia in long distance spread along watercourses may be important. Oospores may form more readily in the forest than in the laboratory, and the role of these oospores in long-term survival is not known. The prevalence of less virulent isolates is not known. It is interesting to speculate about the isolates that are indistinguishable using DNA fingerprints, isozymes, or total proteins, but exhibit differences in virulence. It is possible that passage through certain hosts, storage conditions, or virus infections could have led to reduced virulence. Fundamental questions remain concerning the origin of the species, variability in the native range, and resistance mechanisms of the native host.

Disease Identification and Detection

Port-Orford-cedar root disease is identified in the field by: (a) the rapid death of individual hosts, (b) the almost exclusive occurrence on Port-Orford-cedar, (c) the characteristic distribution of the disease in sites favorable for the water-borne spread of the pathogen, and (d) the distinctive symptoms that *P. lateralis* causes on infected trees (Zobel et al. 1985). Crowns of infected trees first fade slightly or appear somewhat wilted. They subsequently change color from their normal green or blue green to yellowish gold, bronze, reddish brown, and finally dull brown. Symptoms manifest themselves rapidly and tree death occurs quickly in seedlings and saplings during periods when warm, dry weather develops after infection. With such trees, the entire progression of symptoms may occur within two to three weeks. Large Port-Orford-cedar die much more slowly, declining over periods of one to four years. Signs of infection in Port-Orford-cedar roots include loss of luster of root tips, water-soaking of rootlets, and death and decay of roots. The bark on main roots may darken or turn somewhat purplish. Mycelia of the pathogen grow in the inner bark and cambium of hosts, colonizing and killing much of the root systems, and ultimately girdling the main stems in the lower boles. In live Port-Orford-cedar exhibiting crown symptoms, a distinctive cinnamon-colored stain that abuts abruptly against healthy cream-colored inner bark is apparent at or above the root collar (fig. 3.5). This stain, which can be followed down into the roots, is considered diagnostic of infection by *P. lateralis*. Once a Port-Orford-cedar dies, the inner bark of the entire bole turns brown, and it is no longer possible to use presence of staining as an identification tool.

There are several additional techniques available for detecting the presence of *P. lateralis*. The pathogen can be isolated from symptomatic and recently killed trees on a selective medium such as cornmeal agar amended with pimaricin, rifampicin, and ampicillin (CARP medium). Currently, Port-Orford-cedar seedlings



Figure 3.5—Cambial stain on infected Port-Orford-cedar

are used as baits to determine occurrence and quantity of *P. lateralis* inoculum in soil and water. The presence of *P. lateralis* is confirmed by isolation from bait seedlings onto CARP medium. A soil assessment method using tree branchlets floated over water amended with hymexazol and transferred to CARP medium was also developed by Hamm and Hansen (1984).

A Polymerase Chain Reaction (PCR) DNA test for *P. lateralis* is currently being designed, developed and tested at Oregon State University (Winton and Hansen 2000, Winton and Hansen 2001). Early results of trials with this method demonstrate that it can be used to identify *P. lateralis* from both root and stem tissues. Early results indicate this test may become a more sensitive and accurate test than traditional culturing techniques and can reduce by several days the time needed to identify the pathogen. This technique can be performed upon soils by processing foliage baits and may be usable for detecting *P. lateralis* in infested stream water.

Characteristics of Long-Term Infestation

Port-Orford-cedar root disease centers consist of variable-sized groups of dead and dying trees. Port-Orford-cedar is a prolific seed producer, and new regeneration of the host often becomes established in infestation centers. This regeneration usually becomes infected, in turn, resulting in chronic disease expression. Because of its ability to reproduce at an early age, produce large numbers of seeds, and because many trees that occur on sites with characteristics unfavorable for the spread of *P. lateralis* completely escape infection, Port-Orford-cedar has not yet been eliminated by the pathogen in any significant portion of its range. Nonetheless, *P. lateralis* has caused substantial amounts of mortality on individual infested sites and has greatly influenced stand structure by killing large trees and preventing small trees from attaining large size. The disease can greatly influence the ecological roles of Port-Orford-cedar, particularly in streamside areas where conditions are favorable for spread of the pathogen.

Additional Agents Affecting Port-Orford-cedar

Except for *P. lateralis*, Port-Orford-cedar has few significant enemies. Cedar bark beetles (*Phloeosinus* spp., especially *P. sequoiae* Hopkins) infect some trees, but usually only trees with much reduced vigor. They rarely kill trees by themselves, but commonly administer the *coup de grace* to Port-Orford-cedar infected by *P. lateralis*. Port-Orford-cedar is a remarkably decay resistant species. Several decay fungi, including *Phellinus pini* (Thore: Fr.) Pilat and *Heterobasidion annosum* (Fr.) Bref., have been found on Port-Orford-cedar, but are uncommon and appear to have little impact. Grey mold (caused by *Botrytis cinerea* Pers.: Fr.), cypress canker (caused by *Seridium cardinale* (W. Wagner) Sutton & I. Gibson), and root disease (caused by *P. cinnamomi*) are problems in nurseries but rarely cause widespread devastation. Black bears (*Ursus americanus* Pallas) often peel bark and feed on the cambium of trees in early spring, causing extensive local damage to Port-Orford-cedar. Port-Orford-cedars, especially those occurring on drier sites, may succumb to drought during periods of protracted dry weather. Drought may also predispose cedars to attack by bark beetles or woodborers.

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