Survival of *Phytophthora lateralis* in Infected Roots of Port Orford Cedar

E. M. Hansen, Department of Botany and Plant Pathology, Oregon State University, Corvallis 97331-2902, and **P. B. Hamm,** Botany and Plant Pathology, Oregon State University, Hermiston Agric. Res. and Ext. Center, Hermiston 97838

ABSTRACT

Hansen, E. M., and Hamm, P. B. 1996. Survival of *Phytophthora lateralis* in infected roots of Port Orford cedar. Plant Dis. 80:1075-1078.

Short-term and long-term survival of *Phytophthora lateralis* in infected Port Orford cedar rootlets in soil was tested under a variety of conditions. Survival was measured by baiting infected rootlets with cedar foliage baits or by planting cedar seedlings into the infested soil. On the temperature gradient plate, recovery after 7 and 18 days at 10°C was near 100%, but reisolation was sharply reduced from moist soil at 20 and 30°C, and there was no recovery at 40°C. In soil allowed to air-dry at the various temperatures, there was no recovery at 20°C or above. Outdoors, the fungus survived at least 7 days in rootlets buried 10 cm deep in dry soil, and in rootlets on the soil surface, if shaded. There was no recovery from rootlets exposed to the sun. Temperatures did not exceed 25°C in any treatment where the fungus was recovered. Long-term survival of *P. lateralis* in infected cedar roots was tested in litter bags buried in forest and cold frame conditions, and in intact root systems of cedar trees killed by *P. lateralis*. Direct isolation onto selective medium was attempted from forest trees killed at different times in the past. *P. lateralis* was not isolated from any tree dead for more than 2 years. The fungus was recovered by baiting from litter bags after 5 years but not after 6 years, and from root systems in buried pots through the 7 years of the test. Rate of recovery was sharply reduced in the last year in both cases.

Phytophthora lateralis Tucker & Milbrath is an aggressive, introduced pathogen of Port Orford cedar (POC) (*Chamaecyparis lawsoniana* (Andr. Murray) Parl.). Since about 1952, it has been spreading and killing cedar in the native range of the tree in southwestern Oregon and northern California (16), and it was recently confirmed as a pathogen of Pacific yew (1,9). This paper reports on the period of survival of the fungus in roots of killed POC trees in and on forest soils.

Port Orford cedar root disease was first reported in 1923 in the Pacific Northwest from nurseries growing ornamental POC (11,16). It subsequently spread to the native range of the tree. Ornamental nursery production of POC has been largely eliminated; mortality of valuable forest trees causes millions of dollars in timber losses annually; and ecological disturbance in riparian areas and on sensitive ultramafic soils can be dramatic. The fungus is carried upslope and to new areas in mud and debris on vehicles on roads, and spreads downslope in streams and other surface water.

The combination of economic losses and threats to environmental values prompted the U.S. Forest Service to initiate an active program of disease management designed to protect remaining uninfested areas, while promoting the growth of POC on "safe" sites within the general area of infestation (6). Principal tactics in disease management include exclusion of the pathogen through wet season and permanent road closures, sanitation by equipment washing, and reduction of potential inoculum by removing cedar from vulnerable areas adjacent to roads. Limited information on either short- or long-term survival of *P. lateralis* has hampered exclusion and sanitation efforts and slowed attempts to reintroduce the tree into previously infested areas. Resistance has been identified in a few POC individuals (3), and a Forest Service program of selection and breeding for resistance is underway.

P. lateralis is active throughout the cool, wet winter in much of the native range of POC. Summers, however, are warm and dry, and limited evidence suggests that fungus populations decline dramatically. Ostrofsky et al. (10) recovered the fungus from infected roots in moist soil after 20 weeks of incubation at 20°C, 12 weeks at 25°C, and only 2 weeks at 30°C. Survival rates in moist soil and in air-dry soil were compared at 5 and 20°C. Recovery was very low and sporadic in dry soil at both temperatures. *P. lateralis* has a lower temperature optimum for growth and sporulation than many other *Phytophthora* species (12).

P. lateralis is homothallic, but oospores are seldom seen (12). Chlamydospores are abundant, however, and these are found in infected roots (10). The combination of slow growth on selective media and low populations in soil prevents isolation of *P. lateralis* by dilution plating (13). Recovery is accomplished by baiting from the soil organic fraction, including cedar roots, separated from the soil by wet sieving (2,10) or by transferring portions of diseased tissue to selective media.

Our objectives were to measure short-term survival of *P. lateralis* under hot, dry conditions as encountered on forest roads in the summer and to measure the long-term survival of the fungus in diseased roots in forest soils. Short-term survival was tested by exposing inoculum to different combinations of drying and incubation temperature, in incubators and on and in soil. Long-term survival was tested by direct isolations from forest trees dead for different periods of time and by baiting from infected root pieces buried in mesh bags and intact root systems buried in pots for up to 7 years.

MATERIALS AND METHODS

Short-term survival: gradient plate. Naturally infected seedlings from a forest site in southwestern Oregon were excavated, and the roots were cut into pieces about 2 cm long. Root pieces were then mixed with an equal volume of soil collected from the same forest site, and 10-g portions were distributed to plastic petri plates and either sealed to retain moisture or left open. Petri plates were placed on a temperature gradient plate in the dark at 10, 20, 30, and 40°C, then removed and weighed after 7 or 18 days. There were three replicate plates for each time, temperature, and moisture combination. For the 7-day treatments, the organic matter (OM) was separated from the soil in each petri plate and flooded with 100 ml of distilled water, then baited with five 2-cm-long segments of POC foliage (2,8). After 1 week, baits were transferred to corn meal agar with 250 ppm ampicillin, 10 ppm rifampicin, and 20 ppm pimaricin (CARP). The OM from each plate from the 18-day treatments was mixed with vermiculite and transferred to a 600-ml plastic growth tube with a 6-month-old POC seedling. Seedlings were flooded for 24 h, then left for 2 months in the greenhouse for symptom development. *P. lateralis* was confirmed from symptomatic seedlings by direct isolation to CARP. The test was repeated using infected roots and soil from a differ-

Corresponding author: E. M. Hansen
E-mail: hansene@bcc.orst.edu

Accepted for publication 18 June 1996.

Publication no. D-1996-0710-04R

ent site. Recovery was measured by baiting only in the second test.

Short-term survival: soil surface. Infected roots were prepared by inoculating 1-year-old POC seedlings with *P. lateralis*. After the fungus had colonized the root systems (about 6 weeks), roots were chopped and stored moist for 2 months at 5°C. After storage, a portion of the chopped roots was autoclaved to serve as a control. Five-gram samples of chopped roots were transferred to nylon mesh bags and incubated from 19 to 26 September 1994 in a 5°C cold room or outdoors in a cold frame. Bags in the cold frame were on the soil surface either exposed to the sun or shaded, or were buried 10 cm deep in soil, either exposed to the sun or shaded. There were four or five replicate bags of infected roots and control roots at each location. Temperatures in the bags were monitored. After 7 days of exposure, OM was washed and baited as above.

Long-term survival: direct isolation from forest trees. Isolations were attempted from 48 dead POC trees, 5 to 10 cm diameter at the ground line, located along infested roads in southwestern Oregon. Mortality was classed as recent, <1 year old, with foliage green or yellow and a sharp demarcation still evident between diseased reddish phloem tissue below and healthy white phloem above; 1 to 2 years old, with foliage reddish orange to brown and phloem uniformly discolored; and 3 to 5 years old, with gray foliage and dark brown, decomposing phloem. *Phloeosinus* bark beetles were just colonizing the recently killed trees and were often present in the 1- to 2-year dead material, but had already emerged from the oldest class. Trees were cut and roots were excavated and returned to the laboratory for isolation. Segments of phloem (about 2 mm square) adjacent to the cambium were removed along three principal roots, at 5-cm intervals from 10 cm above the root collar to 30 cm below, and were transferred to corn meal agar amended with 10 ppm pimaricin (CMP).

Long-term survival: soil bags and pots. Survival of *P. lateralis* in infested soil was tested in soil bags and in pots with intact, diseased POC root systems. Soil bags and pots were buried on forest sites in southwestern Oregon and in cold frames in Corvallis, OR, and removed for assay at intervals. A preliminary test extended for 30 months, and the main test was sampled over 7 years.

Soil bags contained forest soil mixed with infected cedar roots. Forest soil, collected in southwestern Oregon from beneath POC trees, was transported to a cold frame in Corvallis. POC seedlings were planted in the soil and grown for 2 years, then inoculated with *P. lateralis* by mixing pea broth cultures of the fungus containing chlamydospores into the soil and irrigating heavily. All POC seedlings were dead within 4 months. Seedling tops were removed, and the soil with dead root systems was mixed. Nylon mesh bags were filled with 600 ml of infested soil or with soil collected from the original site in southwestern Oregon beneath healthy POC (control).

Bags for the 30-month test were buried in paired plots at three sites within the range of POC in southwestern Oregon: 1. Coos County Forest near Coos Bay, OR, on a southwest aspect at about 100-m elevation; 2. Powers Ranger District, Siskiyou National Forest, on a southwest aspect at about 1,000-m elevation; and 3. Powers District, on a north aspect at about 400 m. One plot of each pair was in a recent clear-cut, and the second was in the adjacent uncut stand. A fourth set of plots was installed in Corvallis, with one plot in an unirrigated cold frame and the second in an adjacent cold frame that received summer irrigation.

Each plot received 36 infested soil bags buried about 15 cm deep in a single row along the contour and six control bags buried upslope from the infested bags. Six infested bags and one control bag were removed from each plot after 3, 6, 12, 18, 24, and 30 months. OM was separated from each bag by wet sieving, and 5 g of wet weight OM was placed in each of 10 cups for baiting with cedar foliage. Hymexazol in water (25 µg/ml) was added to each cup (2), and five baits were floated on the solution.

Soil bags for the 7-year test were prepared in a similar manner, except that different isolates of the fungus were used. Bags were buried at site 1 (Coos County Forest) and in the irrigated Corvallis cold frame. The test area at site 1 was a recent clear-cut planted with Douglas fir; by the end of the study the young trees had formed a dense, closed canopy over the buried bags and pots. Ten infested bags (nine bags in year 5 from Corvallis) and two control bags were removed in April or May of each year for 6 years. In years 1 to 5, OM was separated from each bag and baited as before. In year 6, the entire contents of each soil bag were transferred to separate plastic growth tubes, and a 6-month-old POC seedling was transplanted into the tube. Soil was flooded for 24 h, and seedlings were held up to 6 months in the greenhouse to allow symptom development.

P. lateralis survival was also tested in the intact root systems of potted, infected seedlings. Four-year-old POC, grown in a soil-based potting mix in 2.5-liter pots, were inoculated with mixed cultures of three isolates of *P. lateralis*. Infected seedlings were transplanted to 11.5-liter pots, which were then filled with soil. Seedlings died within 4 months, and tops were removed. In the 7-year test only, three healthy Douglas-fir seedlings were also planted in half of the pots to test any effects of this nonhost tree on survival of *P. lateralis*. Control pots contained the root systems of healthy POC. Pots were buried to the rims in the clear-cut at site 1 (Coos County Forest) and in the irrigated and unirrigated cold frames in Corvallis. Six pots were removed from each location at each sampling time in the 30-month test; 12 pots (except 10 pots in year 4 from Coos Bay) were removed from each location in each of the first 6 years of the 7-year test. In the seventh year, 22 pots were sampled from Corvallis only. OM was separated and baited as for the soil bags, both in the 30-month test and through year 5 of the longer test. In year 6, OM was separated as before from six of the pots, then divided; half was baited and half was transferred to a growth tube and planted with a POC seedling. Seedlings were planted directly into the other half of the pots without separation of OM. In year 7, seedlings were planted directly into all of the pots, without separation of OM.

Table 1. Effect of temperature and drying on recovery of *Phytophthora lateralis* from infested organic matter after 7 and 18 days in petri plates on a temperature gradient plate

		Closed plates[a]		Open plates[a]	
Temp	Days	Wt. loss (%)	Recovery	Wt. loss (%)	Recovery
10°C	7[b]	0.0	3/3	10.1	3/3
	18[c]	0.4	2/3	9.9	3/3
20°C	7	0.3	1/3	15.7	0/3
	18	0.8	1/3	15.3	0/3
30°C	7	0.8	1/3	15.0	0/3
	18	2.1	0/3	15.8	0/3
40°C	7	0.5	0/3	18.6	0/3
	18	5.7	0/3	17.2	0/3

[a] Moist organic matter (OM) was incubated in closed petri plates sealed with paraffin film or in plates without lids. Plates with OM were weighed before and after incubation, and water loss was calculated.

[b] Seven-day incubation: recovery (plates positive/total plates) was assayed by baiting with cedar foliage baits, three replicate plates with five baits per plate.

[c] Eighteen-day incubation: recovery (plates positive/total plates) was assayed by planting a healthy POC seedling with the OM from each plate, three replicate plates, one seedling per plate.

RESULTS

Short-term survival. Recovery of *P. lateralis* was dramatically reduced at 20°C and above in all tests. Gradient plate re-

sults were similar in both trials, and only the first test is reported (Table 1). At 10°C, there was little difference in survival between open and sealed plates; the fungus was recovered from all replications after 7 days (by baiting), and from five of six replications after 18 days (using the seedling assay). At 20°C and above, however, open plates reached air dryness, and there was no recovery using either assay. In closed plates, the fungus was recovered at reduced frequency at 20°C and from only one bait in one of three cups at 30°C.

In the outdoor test, *P. lateralis* survived the 7-day exposure when buried, whether the soil was exposed to the sun or shaded (Table 2), but the fungus was recovered from only half of the total number of baits for the bags exposed on the soil surface in the shade and was not recovered at all from the inoculum exposed on the soil surface to the sun. Temperatures in the buried bags and in the shaded bags on the surface did not exceed 25°C during the test, whereas bags exposed to the sun exceeded 40°C for 4 or more hours each day. Water loss was not measured, but buried bags remained moist to touch while bags on the surface dried quickly.

Long-term survival: direct isolation. *P. lateralis* was isolated from 12 of 14 recently killed trees. Isolations from discolored portions of the bole were more successful than isolations from the roots. *Phytophthora* was not recovered from the bole above the margin of discoloration. Recovery from trees dead 1 to 2 years was lower (13 positive trees of 21 attempted). More successful isolations came from roots than from bole tissue, probably because of the effects of bark beetle colonization of the stem. *P. lateralis* was not recovered by direct isolation from any of the 13 sampled trees that had been dead more than 2 years.

Soil and pots. In the 30-month test, *P. lateralis* was recovered from all soil bags and all intact cedar root systems in pots at all sample times at all locations (data not shown). There was no evident reduction in viability except in the 24- and 30-month soil bag samples. The average number of 5-g OM samples positive per bag decreased from 10 out of 10 at time 0, to 7 of 10 after 30 months. The proportion of baits positive decreased from 90–100% to 50–60%. Recovery rates tended to be lower in clear-cuts than in forested locations, and lower in the summer dry cold frame than in the irrigated plot, but differences were small. No *Phytophthora* was recovered from control bags or pots at any time.

In the second survival test, *P. lateralis* was still viable and infective in some samples after 7 years (Table 3). At 4 years, the fungus was recovered from all Corvallis soil bags and 66% of the 5-g samples from those bags, and from 8 of 10 Coos Bay soil bags, including 21% of the 5-g samples. Recovery from soil bags fell dramatically in year 5 at both locations, and the fungus could not be detected with the live POC seedling assay in year 6, the last year of sampling.

Recovery from the intact POC root systems in pots followed a similar trend. After 4 years, the fungus was recovered by baiting from all of the Corvallis pots, and from nine of 10 of the Coos Bay pots. In year 6, detection of *P. lateralis* was similar with both seedling and baiting assays. The fungus was recovered in year 6 from seven of 12 Corvallis pots and nine of 12 Coos Bay pots. In year 7 only the seedling assay was used and the fungus was isolated from five of 22 pots. Through year 6, *P. lateralis* was isolated with a higher frequency from pots without Douglas-fir seedlings than from pots in which seedlings had been planted, but in year 7, all recoveries were from pots with Douglas-fir seedlings. No *Phytophthora* was recovered from any control bag or pot at any time during the study.

DISCUSSION

P. lateralis survives and remains infective in the absence of living host tissue in a range of natural environments for at least 7 years following artificial inoculation. Survival for at least 6 years has been shown previously for several other *Phytophthora* species (7), including *P. cinnamomi* (15), and an unidentified *Pythium* species was recovered from air-dry soil after 12 years (4).

Previous field observations have suggested that the period of survival of *P. lateralis* might be 3 years or less. Ostrofsky et al. (10) described young, apparently healthy cedar trees found growing among trees killed earlier by the fungus. In a direct test of survival, Kliejunas (5) sampled for *P. lateralis* around six POC trees recently killed by the fungus in a northern California forest. He collected a single 0.5-

Table 2. Recovery of *Phytophthora lateralis* from infected root fragments after 1 week in soil bags on the soil surface or buried, exposed to sunlight or shaded

Treatment	Temperature (C)		Recovery[a]	
	Max.	Min.	Bags	Baits
Buried, shade	19	17	5/5	25/25
Control[b]	19	17	0/4	0/20
Buried, sun	24	19	4/4	18/20
Control	24	19	0/4	0/20
Surface, shade	25	13	5/5	12/25
Control	25	13	0/5	0/25
Surface, sun	46	11	0/4	0/20
Control	46	11	0/4	0/20

[a] Recovery is expressed as the number of samples positive (soil bags or cedar foliage baits)/number of samples assayed. Five bags were incubated in each treatment. Root fragments were washed and baited with five cedar baits per bag.
[b] Control bags contained autoclaved root fragments.

Table 3. Long-term survival of *Phytophthora lateralis* in infested soil in bags or in infected cedar root systems in pots buried at two locations and sampled annually. Survival (% samples positive) was assayed by baiting extracted organic matter with cedar foliage baits or with intact seedlings

Year	Soil bags[a]						Pots[b]					
	Corvallis			Coos Bay			Corvallis			Coos Bay		
	Bags	Cups	Baits	Bags	Cups	Baits	Pots	Cups	Baits	Pots	Cups	Baits
0	100	97	...	...	...	...	100	97	...	...	...	...
1	100	51	28	100	83	58	100	84	81	100	98	95
2	100	82	66	100	62	46	100	89	88	100	93	...
3	100	74	49	100	70	44	100	98	92	100	93	86
4	100	66	38	80	21	10	100	49	31	90	81	73
5	67	18	8	30	3	1	92	87	79	92	49	40
6[c]	0	...	...	0	...	...	58	37	19	75	57	49
7[d]	NT			NT			23	...	...	...	...	...

[a] Nine or 10 soil bags were removed annually from each location through year 5. Twenty-four bags were removed in year 6.
[b] Ten or 12 pots were removed annually from each location through year 6. Twenty-two pots were removed in year 7.
[c] In year 6, a cedar seedling was planted in the contents of each soil bag. No baiting assays were done from soil bags. Pots were assayed by baiting as before, and by planting a cedar seedling in the remaining portion of the extracted organic matter. Only results from the baiting are presented here.
[d] In year 7, soil bags were not tested (NT). Pots were assayed only by planting a cedar seedling in each pot.

liter soil sample from each tree, separated OM, and baited with POC foliage, using the same techniques as those used in the present study. *P. lateralis* was recovered from all six sites at the beginning of the study, but from only two sites 3 months later, and not at all after 3 years. The longer survival demonstrated by baiting in the present study is probably a result of increased sampling intensity and high initial concentrations of diseased roots in soil bags and pots.

Our failure to recover the fungus by direct isolation from naturally infected trees dead for 3 or more years reflects the same limitation of low propagule numbers that Kliejunas (5) encountered, as well as limitations of the isolation technique. Dead cedar roots are quickly colonized by saprophytic fungi, including *Pythium* and *Mortierella* species tolerant of the antibiotics used in the selective medium.

In the present study, recovery rate of *P. lateralis* was associated with the volume of material sampled, especially the amount of POC root fragments in the sample. Recovery from the soil bags was possible by baiting after 5, but not 6, years. The amount of organic matter recovered from the bags declined steadily through the study. In the first test, for example, about 40 g of OM was recovered from each soil bag at time 0, but only 20 g after 30 months. In the second test, the amount of OM at 6 years was insufficient for the baiting test, so seedlings were planted in the whole soil. *P. lateralis* was not recovered. The pots started the tests with intact, infected root systems of 4-year-old POC seedlings, and sufficient material remained for testing through the duration of the study.

These results suggest that the fungus survives in root pieces and loses viability as those pieces decompose in the soil. This supports the conclusions of Ostrofsky et al. (10) that *P. lateralis* is a root-inhabiting fungus, with little saprophytic colonizing ability. They observed chlamydospores in infected root tissue, and it is possible that oospores are formed also (12).

It is difficult to recover *P. lateralis* from soil (13). The fungus grows slowly and does not compete well in culture with other fungi that grow on the selective media employed. It is seldom isolated on soil dilution plates from naturally infested soil, but can be recovered by baiting from separated OM. This, plus the confinement of the fungus to root fragments, has precluded development of a quantitative assay, but the reduction over time in the number of 5-g subsamples with positive baits and in the proportion of baits colonized suggests a gradual reduction in the number of viable propagules. The reduction probably starts from death of the host, but is not evident so long as sufficient inoculum remains to colonize all of the baits. Since baits are presumably infected by zoospores released from sporangia formed on infested root fragments in the flooded OM, zoospores from a single sporangium might be sufficient to colonize all of the baits in a cup.

It is likely that survival period varies in different environments. The Coos Bay and Powers sites used in this study are in the heart of the POC range, with moderate climates compared to more extreme environments where cedar grows at higher elevations and farther south. It seems evident, however, that *P. lateralis* can survive without its host for much longer than the normal 1- to 2-year interval between harvest of one stand generation and establishment of the next. Reestablishment of POC on diseased sites will require prolonged periods without a living host, as well as protection against reintroduction of the fungus. The ability of the relatively shade-tolerant POC to grow as an understory tree may allow replanting after the fungus has died from infested sites.

The demonstrated sensitivity of *P. lateralis* to warm, dry conditions is consistent with other *Phytophthora* studies (14), including those of Ostrofsky et al. (10), with *P. lateralis*. Seasonal fluctuations in populations are related to host availability, temperature, and water availability for zoospore release and transport. In the range of POC, *P. lateralis* is active through the cool and wet fall, winter, and spring seasons. Summers are warm and dry, but even 10 cm below the soil surface, conditions are moderated enough to allow survival of the fungus. In a recent field test of the effects of fire on survival of *P. lateralis* (Greg DeNitto, USDA Forest Service, Redding, CA, *unpublished*), the fungus was recovered by baiting from four of eight soil samples collected before burning, and from the same four positive sample sites after burning. Soil temperatures at a depth of 10 cm did not exceed 38°C in this test.

A key facet of POC root disease management is seasonal closure of unpaved roads in critical areas. The premise is that infested soil is more likely to be transported as mud on wet roads than as dust on dry roads. The demonstration of very limited survival at 30 or 40°C, especially in dry OM, and on soil surfaces exposed to the sun, extends the rationale for limiting operations to the dry season on these roads. Road surface temperatures in southwestern Oregon rise above 40°C within minutes of exposure to summer sun (data not shown). Air temperatures beneath forest stands with POC seldom exceed 30°C, however, and soil temperatures remain below 20°C on most sites (16). This fungus is well suited for survival in forest soils in the range of POC, although opportunities for spread appear to be strictly limited in the summer months.

ACKNOWLEDGMENTS

This work was supported by the USDA Forest Service through the Pacific Northwest Forest and Range Experiment Station. We thank John Kalafarski for his work on direct isolation of *P. lateralis* from killed trees.

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