Operational Program to Develop *Phytophthora lateralis*-Resistant Populations of Port-Orford-cedar (*Chamaecyparis lawsoniana*)

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Abstract

Port-Orford-cedar (*Chamaecyparis lawsoniana* (A. Murr.) Parl.) (POC) is a long-lived conifer native to northwestern California and southwestern Oregon. It has been widely used in horticulture in both western North America and elsewhere. The accidental introduction of the non-native pathogen *Phytophthora lateralis* into North America and Europe has raised concerns about the future viability of POC in some forest ecosystems, in managed forests, and in horticultural settings. Fortunately, some level of natural genetic resistance to *P. lateralis* exists in POC. Utilizing this genetic resistance in reforestation and restoration of POC offers considerable benefits without the negative side-effects of alternatives. In 1997, the USDA Forest Service and USDI Bureau of Land Management began a large operational program to develop populations of POC with genetic resistance to *P. lateralis*. With essential ongoing pathology support from Oregon State University, this resistance program has advanced rapidly. The program goal includes developing orchards for production of resistant seed, while maintaining genetic variation and adaptability within the species. Using classical selection and testing techniques, over 12,600 initial field selections have been made, resistance screening protocols refined, 13 breeding zones delineated, field trials established, eight seed orchards started, and resistant seed produced and being used for some breeding zones. Early, short-term testing in the greenhouse of orchard seedlots shows a 30 percent or higher survival than woods-run seedlots. In greenhouse testing, survival among individual susceptible and resistant families varies from 0 to 100 percent, and at least two types of resistance are apparent. Field trials have been established and early results are encouraging, but much longer monitoring is needed to examine a full range of sites for efficacy and durability of resistance under different environments and a changing climate. The recent finding of *P. lateralis* in Europe and Taiwan warrants further investigation into the pathogenicity of these isolates on resistant POC. The biology of POC and the concerted efforts of all those involved have made this fast moving resistance program one of the few involving non-native pathogens to produce seed for restoration and reforestation. Planting the less susceptible seedlings will increase the frequency of resistance in areas affected by *P. lateralis* and help to establish a new balance in affected ecosystems.

Key words: Port-Orford-cedar, *Chamaecyparis lawsoniana*, *Phytophthora lateralis*, resistance program

Introduction

Port-Orford-cedar (*Chamaecyparis lawsoniana* (A. Murr.) Parl.) (POC) is a large, long-lived conifer species native to southwestern Oregon and northwestern California (figs. 1 and 2) (Betlejewski et al. 2011; USDA FS and USDI BLM 2003, 2004; Zobel et al. 1985). It has also been widely utilized in urban plantings in North America, Europe, and elsewhere, where it is often called Lawson's cypress. However, the introduction of a root disease, caused by the non-native pathogen *Phytophthora lateralis* (Tucker and Milbrath), in North America and Europe has caused high mortality in some forest ecosystems and has limited POC's use in forest plantings and in horticulture (Betlejewski et al. 2011, Casavan et al. 2003, Robin et al. 2011, Sansford 2011, Zobel et al. 1985). *Phytophthora lateralis* is spread primarily via water and soil. All sizes and ages of POC can be killed by *P. lateralis*. POC is the only species in North America currently known to be highly susceptible to *P.*

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lateralis, although Pacific yew (*Taxus brevifolia* Nutt.) is occasionally killed (DeNitto and Kliejunas 1991).

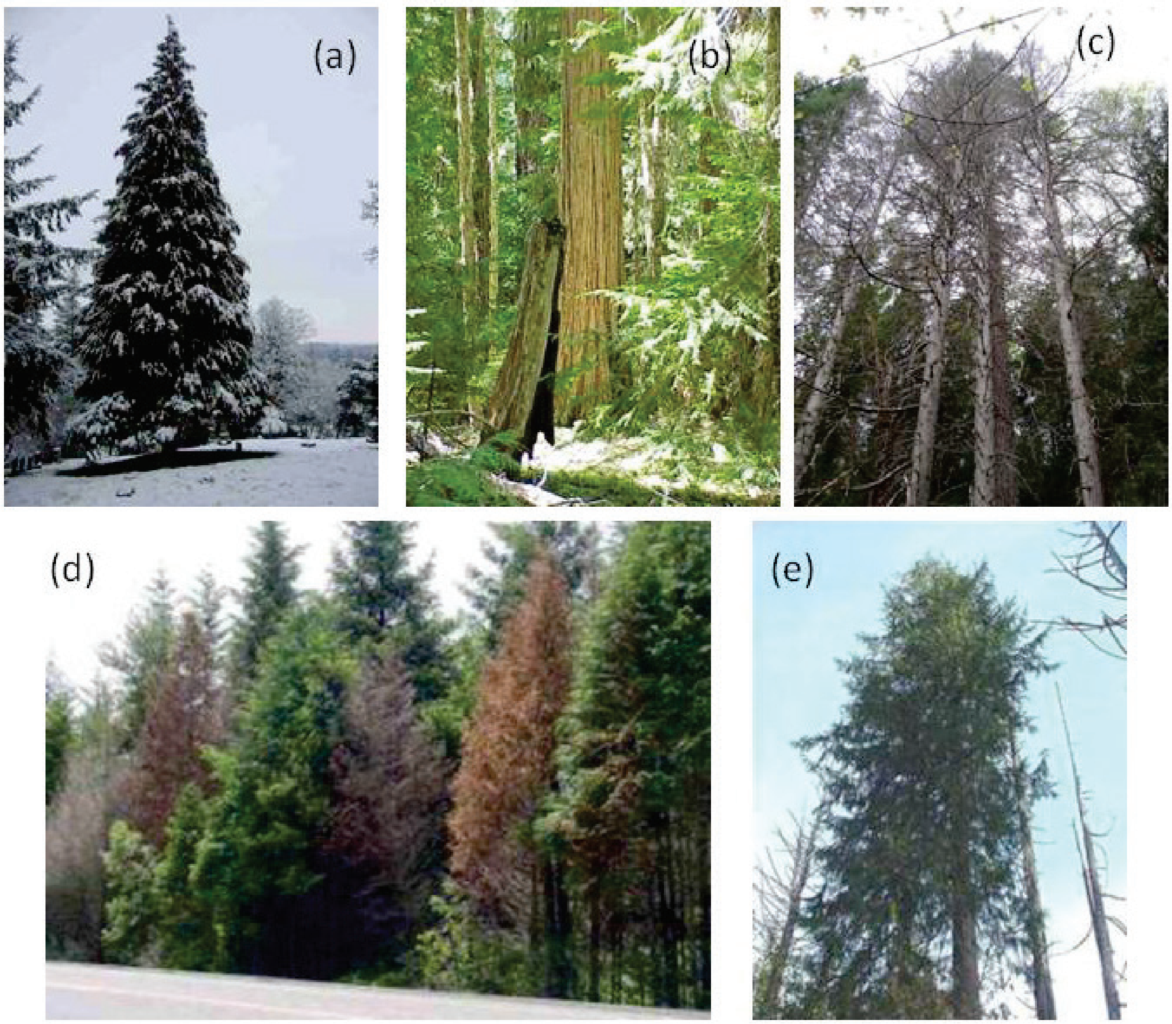

Figure 1—Port-Orford-cedar (a) tree in urban area, (b) large, healthy tree in southern Oregon, (c) dead trees in forest along a creek in southwest Oregon, (d) dead and dying trees along Highway 101 in southwest Oregon, (e) resistant parent tree (510015) surrounded by dead Port-Orford-cedar. (Photo credits: Richard Sniezko, a to d; Chuck Frank, e)

The native range of POC encompasses lands managed by many governmental and private organizations and individuals. In this region, POC occurs widely on lands managed by the USDA Forest Service (USFS) and USDI Bureau of Land Management (BLM). The USFS and BLM have implemented an integrated strategy to manage POC ecosystems on their lands in the presence of *P. lateralis*, including: measures to exclude the pathogen from areas not yet affected, sanitation of some infested areas, and minimizing planting sites of highest hazard, such as wet, low-lying areas (Betlejewski et al. 2011, USDA FS 2004, 2006; USDI BLM 2004). However, genetic resistance is a species' natural line of defense against potentially damaging biotic and abiotic agents, and resistance to *P. lateralis* is necessary to retain POC in some ecosystems and to help ensure its continued use in managed forests and horticulture. Fortunately, early work examining possible genetic resistance in POC (Hansen et al. 1989, Sniezko et al. 2003) showed enough promise to begin an operational program to develop resistant populations of POC. The production of seed from seed orchards containing genetically-resistant parents offers land managers the opportunity to continue to use POC in reforestation and restoration. Until recently, however, few operational programs have been undertaken to develop genetic resistance to a non-native pathogen and even fewer are currently producing resistant seed (FAO 2008, Sniezko 2006). In this paper, we provide an update on the substantial progress made since 1997 in the *P. lateralis* resistance program for Port-Orford-cedar.

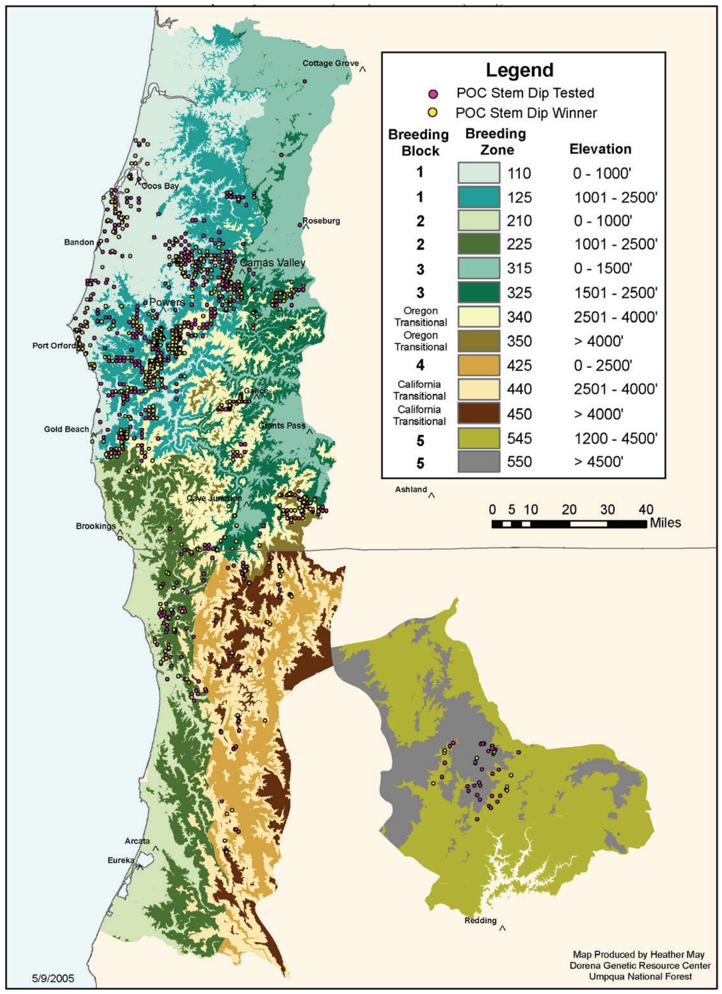

Figure 2—Map showing the 13 breeding zones in the natural range of Port-Orford-cedar and the geographic distribution of field selections being tested for *Phytophthora lateralis* resistance.

Overview

The USFS and BLM program to develop populations of Port-Orford-cedar with genetic resistance to *P. lateralis* expanded to an operational level in 1997. Earlier work at Oregon State University (OSU) and by the USFS and BLM focused on confirming the presence of genetic resistance, selecting the first several hundred candidate trees displaying reduced susceptibility, refining screening techniques for resistance, and developing tree improvement protocols necessary to implement an operational program for this species. The USFS provides overall design for the resistance program and oversees most operational phases, including coordination of field trial establishment, control pollinations for breeding to enhance resistance, data analysis, and seed orchard development for producing resistant seed for reforestation and restoration. Oregon State University provides essential pathology support, including work on biology of the pathogen as well as establishment and monitoring short-term resistance screening trials. The USFS and BLM provide genetics expertise, funding and personnel for the resistance program, sites for field trials, and have identified most of the field selections. The BLM has established and maintains a gene conservation clone bank. Other federal, state, and private cooperators have supported the program by providing tree selections for resistance testing and sites for field trials. Summaries of genetic and resistance work in the operational program through to 2001 are reported elsewhere (Kitzmiller et al. 2003, Sniezko 2004; Sniezko and Hansen 2000, 2003; Sniezko et al. 2003), but significant updates on delineation of breeding zones, seed orchard development, seed availability, testing protocols, and understanding of resistance have occurred over the intervening 10 years.

Integrated Strategy

Developing populations of POC with resistance to *P. lateralis* will be key to increasing success in reforestation and restoration efforts. At this stage, to help maximize the progress in disease resistance, the POC program has focused only on genetic resistance and has not selected for increased growth rate or other traits that may be of interest in reforestation.

POC is a long-lived species that spans very diverse environments (e.g., soils, climate) (Zobel et al. 1985). It is therefore essential to include both genetic diversity and adaptability considerations in the implementation of the resistance program to ensure resulting seedlings will be adapted to current conditions, as well as to buffer the species against a changing climate and other possible insect or pathogen problems.

To help ensure adaptability of future reforestation and restoration plantings, the natural range of POC is currently divided into five breeding blocks, and a total of 13 breeding zones (fig. 2). A breeding block designates the geographic area that envelops a number of breeding zones. The preliminary breeding blocks and zones serve to guide seed transfer and associated breeding activities, where genetic reproductive materials (such as seed, seedlings, and cuttings) are procured or produced in a breeding program, and then subsequently deployed (seeded or planted). The preliminary breeding blocks and zones were updated in 2005 by the BLM and USFS, and were delineated on the basis of various short-term and long-term studies and data. Breeding zones are represented by an elevation band within a respective breeding block. Further analyses of existing long-term common garden studies (fig. 3) that supplement the earlier analysis of 7-year-old data by Kitzmiller (2006), or other future studies, will be used to refine the breeding blocks/zones over time. Seedlots may also be delineated in the future within any respective breeding zone on the basis of source soil type. The tree species occurs on both ultramafic (serpentine) and other soil types (Zobel et al. 1985). A number of plant species have differentially adapted to these distinct soil types (Linhart 1995), but the degree to which POC is specifically adapted is not known.

Since 1997, over 12,600 field selections have been made to help maintain genetic diversity during the subsequent testing and selection process for parents for the seed orchards and for future breeding. Many of the selections have been made in areas where mortality from *P. lateralis* is evident, while others represent random selections in areas not yet impacted. Selections have been made throughout the range of POC, with more selections in the areas where the species is more prominent (fig. 2). Field selections are tested in several steps for resistance (Hansen et al., Methods for screening Port-Orford-cedar for resistance to *Phytophthora lateralis*, these proceedings; Sniezko et al. 2003) with the final selections placed in seed orchards or breeding orchards. Based on their rating in the stem dip test, approximately 10 percent of the original field selections have been retained for further resistance evaluation using a root dip testing method (Hansen et al., Methods for screening Port-Orford-cedar for resistance to *Phytophthora lateralis,* these proceedings; Sniezko et al. 2003). The root dip testing of much of this subset of parental selections (or their progenies) has been completed. Results from this test are used to determine which materials are placed into orchards and used for breeding.

Figure 3—Port-Orford-cedar: (a) measuring height in 2011 in1996 POC provenance trial in northern California; (b) different color and form for multiple copies of two different parent trees in the Tyrrell clone bank; (c) clone bank. (Photo credits: Chuck Frank, a; Richard Sniezko, b and c)

In general, the disease-resistance program involves a sequence of steps to identify resistant parent trees and to propagate those parent trees in seed orchards to provide seed for reforestation and restoration (fig. 4). In the first cycle of selection and testing, candidate parent trees are selected from forest stands within the range of POC (fig. 2). These selections are tested for resistance in short-term tests (for methods, see Hansen et al., Methods for screening Port-Orford-cedar for resistance to *Phytophthora lateralis*, these proceedings; Sniezko et al. 2003) and resistant parents or progeny are retained for orchard development and breeding. Control crosses (selfs and outcrosses) are used to generate progenies for testing resistance and for further selection to increase resistance. A project to examine the genetic diversity within the orchard populations using molecular markers is underway.

Resistance Testing

Efficient, short-term resistance testing is a key step in any operational resistance program. It permits the rapid identification of parent trees to be included in the production orchards or for further breeding. Several short-term tests have been used (Hansen et al., Methods for screening Port-Orford-cedar for resistance to *Phytophthora lateralis*, these proceedings; Sniezko et al. 2003), but a greenhouse root dip test of seedling families or of rooted cuttings of parent trees provides the most information on resistance. The seedling test is preferred over that of rooted cuttings of older parent trees which sometimes give anomalous results. The root dip testing of seedlings can identify differences in survival among families with qualitative resistance, as well as differences in time of mortality among families and the substantial within-in family variation in resistance when quantitative resistance is present (Sniezko 2004). In the POC program, these differences became much more apparent beginning with the 2005 testing, when the duration of the assessment period for the root dip test was expanded from less than a year to up to 3 years.

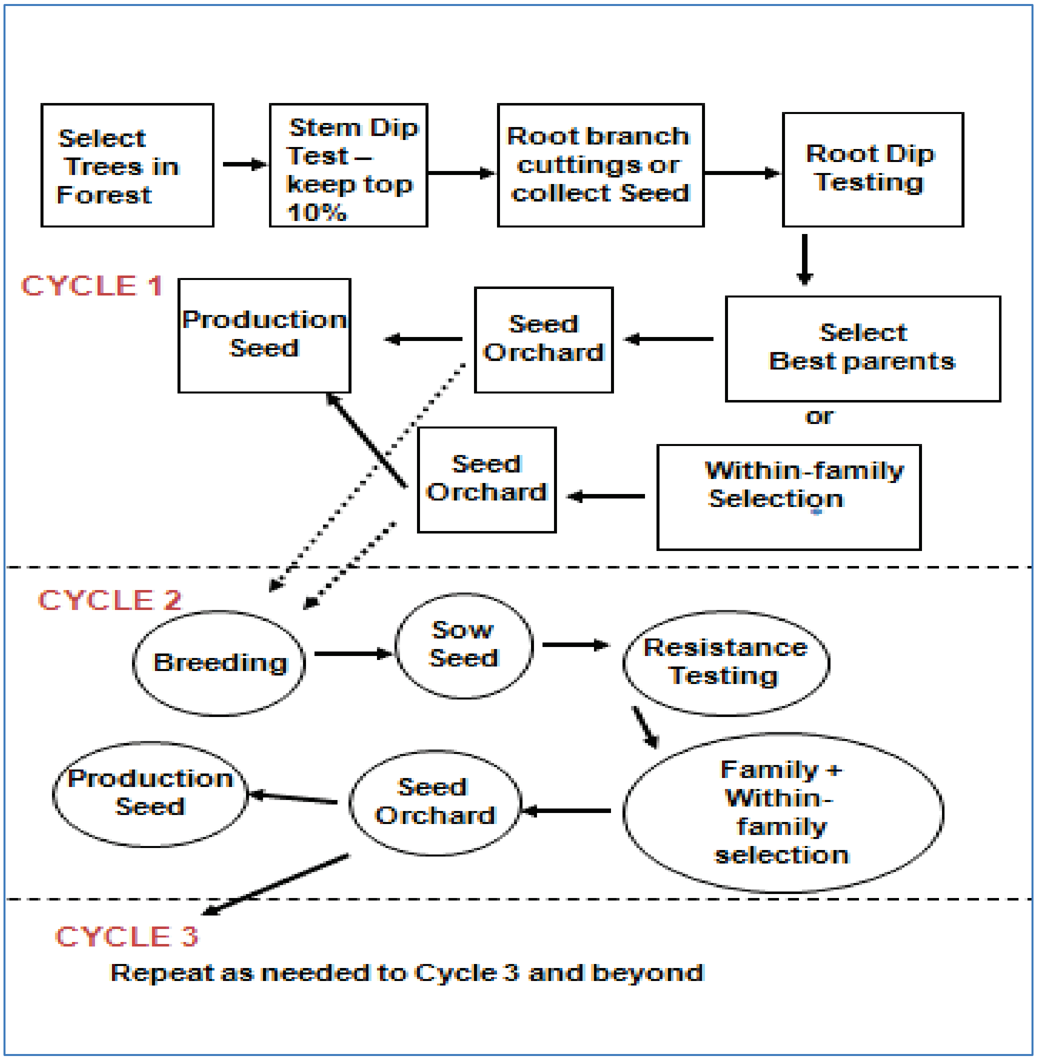

Figure 4—Selection and breeding cycles for developing *Phytophthora lateralis* resistant populations of Port-Orford-cedar for reforestation and restoration.

Both wind-pollinated (especially if collected from forest stands) and control-crossed families are used in the root dip testing. Many POC are somewhat self-fertile (Sniezko et al. 2003), and self-pollinated families have been used routinely for resistance testing in the last few years. In the short-term root dip test, families can vary in survival from 0 to 100 percent (fig. 5) (Sniezko 2004). One or more high-susceptible controls are normally included to provide a baseline to compare all families. The susceptible control families usually reach 100 percent mortality in 100 to 150 days after artificial inoculation (fig. 5). Current efforts are primarily focused on finishing the root dip resistance testing of the forest selections and adding these parents (or their progenies) to the orchards. Other efforts include increasing resistance through breeding, gaining further understanding of the types of resistance and their inheritance, and examining the level of genetic resistance present in wind-pollinated seedlots from the orchards.

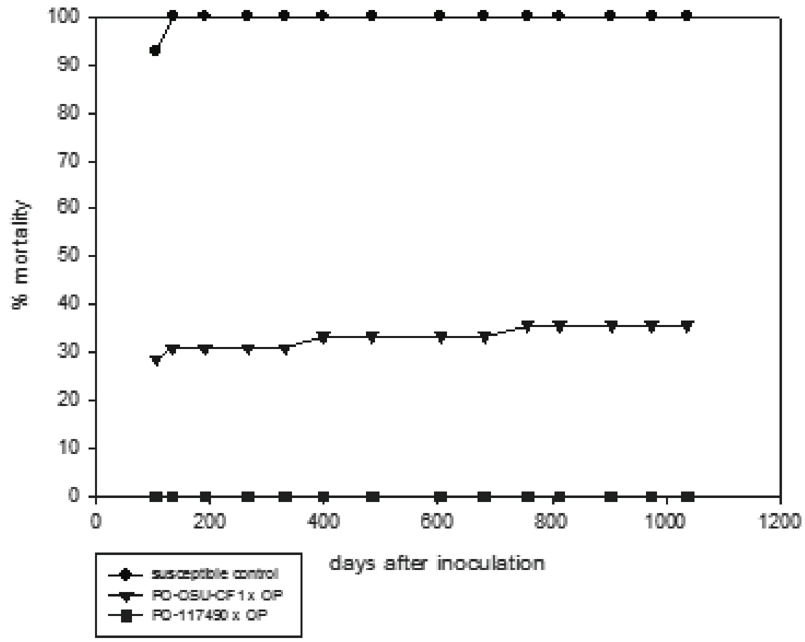

Figure 5—Percent mortality in root dip testing for a susceptible control Port-Orford-cedar family and two resistant families.

The greenhouse root dip test has provided a relatively quick assay to identify resistance in POC. In the root dip test, it appears that at least two types of resistance are present, a qualitative one that identifies some families with high survival (fig. 5) and a quantitative one in which there is often very wide variation within a family for the rate of progress of *P. lateralis* in reaching the root collar (Sniezko, unpublished data). Expansion of the assessment period of the root dip test in 2005 from approximately 9 months to up to 3 years more clearly identifies those families with qualitative resistance, quantitative resistance, or both. Families with each type of resistance are now under field test. Breeding to combine resistances is also underway.

Research on a small subset of resistant and susceptible families from the operational program was undertaken to examine the underlying nature of the resistance in POC. Symptom development on resistant trees included cell wall thickening, cell collapse, and deposition of electron-dense materials around hyphae; all reactions consistent with a hypersensitive response in the host (Oh and Hansen 2007, Oh et al. 2006). Further work to discern the number of resistance mechanisms, their inheritance, the underlying nature of resistance, and its durability is warranted.

Durability of Resistance

Genetic variability within North American isolates of *P. lateralis* is small, likely due to a genetic bottleneck from the original introduction of this pathogen from elsewhere (Goheen et al. 2003), and this may bode well for durability of resistance. Recorded survival for a decade or more of many of the initial field selections in areas of high *P. lateralis*-caused mortality is encouraging (fig. 1e). These trees could serve as permanent plots to help monitor resistance. In addition to the root dip testing, short-term testing using raised beds infested with *P. lateralis* has been used to test resistance (Hansen et al., this proceedings). No change in efficacy of resistance is apparent in continued use of these raised beds for more than a decade (Sniezko, unpublished data). However, the relatively recent findings of *P. lateralis* in Europe (Sansford 2011) and Taiwan (Brasier et al. 2010, Webber et al. 2011) raise concerns about potential increased pathogenicity from new introductions or the evolutionary potential of current isolates. Testing the efficacy of POC resistance to these different isolates is planned.

Long-term field testing of a subset of the resistant selections is essential to assay resistance under a variety of field conditions as well as to continue to monitor durability of resistance. An extensive set of field trials have been established, and early results from the first ones are encouraging (Sniezko et al. 2006; Sniezko et al., Nine Year Survival of 16 *Phytophthora lateralis* resistant and susceptible Port-Orford-cedar families in a southern Oregon field trial, these proceedings). However, it is essential that these trials continue to be monitored to assess the efficacy and durability of resistance in long-lived POC.

Seed Orchards

Resistant seed can be collected from selected trees in the forest and from seed orchards. Seed orchards offer several potential advantages, including increased genetic resistance and relatively easy production of large quantities of resistant seed from a diverse array of parents. For POC, seedlings from wind-pollinated containerized seed orchards (CSOs) are the principal source of reproductive materials for reforestation and restoration (fig. 6). The biology of POC is very conducive to the use of CSOs for the production of large quantities of seed at an early age (Elliott and Sniezko 2000, Sniezko et al. 2003). Branches from resistant trees or tops clipped from 1-year-old resistant seedlings are used to produce rooted cuttings which are then placed in pots in a greenhouse orchard. The CSO technology for POC has allowed for a much shorter time interval between identification of resistant trees and operational production of seed. With the ability to induce seed cones and pollen cones, seed can be produced within 5 years of orchard establishment. For some breeding zones, resistant seed has been available since 2003. In addition, breeding POC to enhance resistance can be done within several years of identifying resistant trees. Seed orchards have been started for eight of the 13 breeding zones (table 1). In these orchards, rooted cuttings of resistant clones have been propagated

Figure 6—Containerized seed orchards at Dorena Genetic Resource Center: (a) seed orchard, (b) abundant cone production on orchard tree, (c) control pollinations. (Photo credits: Richard Sniezko)

and placed together by breeding zones in the greenhouses. The current number of parents per orchard varies from five to 115 (table 1). Ongoing priorities include screening more forest selections for potential inclusion into orchards for additional breeding zones and to increase the number of parent trees in existing orchards as well as to retest some of the early orchard selections to confirm their resistance. The utilization of containerized seed orchards allows for easy updating of orchards as resistance screening results become available. Rooted cuttings of many of the most resistant trees have also been used to establish a clone bank for long-term preservation (fig. 3).

Table 1—Number of *Phytophthora lateralis*-resistant Port-Orford-cedar parents in containerized seed orchards (CSOs) for eight breeding zones as of 2011

Breeding zone[a]	Number of parents
110	60
125	115
210	10
225	9
325	16
340	68
440	5
450	8

[a] See fig. 1 for delineation of 13 breeding zones; No CSOs for BZs 315, 350, 425, 545, 550.

The first-generation seed orchards are wind-pollinated and produce a genetically heterogeneous mix of seed with an intermediate level of resistance. A short-term greenhouse root dip trial, inoculated in 2004, of several orchard breeding zones, showed 30 percent or higher survival in many zones over woods-run seed (fig. 7) (Sniezko et al. 2005). Results from short-term tests like the greenhouse root dip test probably represent an upper limit to resistance from the current generation of orchards, and confirmation of the level under field conditions is needed. Field tests on sites of moderate to extreme disease hazard are essential to determine any limits on the use of resistance and the level of survival to be expected over time. Seedlots from several orchards have been included in recent field tests and results are pending. This field data will be essential information to guide activities of land managers interested in utilizing resistant POC. Early results from some of the first field trials using individual half-sib and full-sib families show encouraging results (Sniezko et al. 2006; Sniezko et al., Nine year survival of 16 *Phytophthora lateralis*-resistant and -susceptible Port-Orford-cedar families in a southern Oregon field trial, these proceedings), but as with any long-lived species, these trials need continued monitoring. Information on the disease hazard of sites would also be useful to managers planning on utilizing resistant POC. Until more field results are available, planting sites should be chosen carefully, avoiding the highest risk sites such as low-lying wet areas down slope from infested areas. The impact of changing climate on the spread of *P. lateralis* or the efficacy of resistance is unknown and warrants investigation. The level of genetic resistance in advanced-generation orchards should increase with breeding and subsequent testing and selection. The containerized orchards serve to meet seed needs for both the Forest Service and BLM. In addition, the Oregon Department of Forestry (ODF) has acquired resistant seed for its seed bank (Oregon Forest Tree Seed Bank) to serve the needs of other landowners. The ODF has filled requests for seed from nurseries and non-federal landowners from 2003 to 2011 (Larry Miller, Oregon Department of Forestry, personal communication). Over 3.85 kg of seed (385,000 to 452,000 seed per kg, approximately 60 percent filled seed) has been dispersed (table 2). Most of the seed need has been for the western most portions of Oregon (Breeding Zones 110 and 125, fig. 1; table 2).

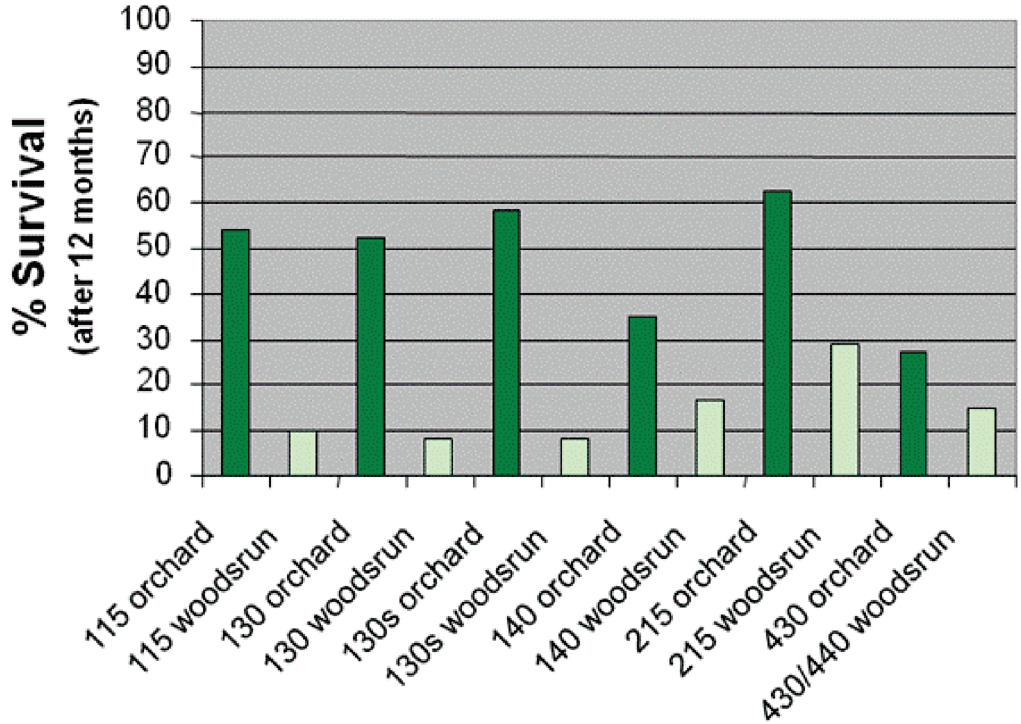

Figure 7—Port-Orford-cedar survival of orchard seedlings versus ‘woodsrun’ seedlings for five breeding zones (from 2000 zones) in a 2004 greenhouse root dip test for *Phytophthora lateralis* resistance.

Resistant seed is now being used by federal and non-federal land managers for reforestation and restoration (figs.8 and 9; table 2). Due to changing management practices on some federal lands, including reduced timber harvest, opportunities for using resistant POC seed in restoration and reforestation are now more limited, and the use of the highest level of resistance possible would aid efforts to retain POC in ecosystems while allowing resistance genes to spread as trees reach reproductive age. On USFS and BLM lands, plantings are often in areas that have been burned by wildfires (USDA FS 2010). Plantings on non-federal lands will facilitate more diversely managed forests, while also setting up opportunities via natural pollen and seed dispersal for increasing the spread of resistance genes to adjacent USFS or BLM lands. Increasing the frequency of genetic resistance over the landscape will help ensure that POC remains a viable component in forest ecosystems impacted by *P. lateralis*.

With the discovery of a number of POC parent trees with resistance to *P. lateralis*, there is revived interest in POC in the horticultural sector. The only option currently available, and limited in use, is grafting established cultivars onto the one resistant parent that has been made available for this purpose. However, the resistance screening of parent trees and their progenies from throughout the range of POC and crosses among them offers additional possibilities. In order to meet the different objectives for horticulture, materials should be carefully evaluated for the range of usage anticipated.

Figure 8—Volunteers from several community groups and a USDA Forest Service biologist planting 900 Port-Orford-cedar (POC) along Grayback Creek in southern Oregon in 2008. This planting project will help restore a riparian area used by salmon and steelhead and also serve as a test of resistant *P. lateralis*-resistant POC. (Photo credit: Scott Kolpak)

Figure 9—Port-Orford-cedar technical committee visiting 2011 planting of resistant POC along trail at South Slough National Estuarine Research Reserve in western Oregon. (Photo credit: Richard Sniezko)

Table 2—Seed (grams) requested by non-federal landowners[a]

	Breeding Zones[b]							
Year	**110**	**115**	**125**	**130**	**210**	**215**	**430**	**Total**
2003	-	172	-	-	-	-	-	172
2004	-	340	-	-	-	-	-	340
2005	-	458	-	254	-	-	-	712
2006	-	481	-	-	-	-	73	554
2007	-	503	-	-	-	50	-	553
2008	-	-	-	-	45	-	-	45
2009	68	-	340	-	-	-	-	408
2010	-	-	340	-	-	-	-	340
2011	386	-	340	-	-	-	-	726
Total	454	1954	1020	254	45	50	73	3,850

[a] Data provided by Larry Miller, Oregon Department of Forestry.
[b] Breeding zones were reduced and reorganized in 2005 (see fig. 1 for current zones).

Other Possible Future Activities

If funding permits, other components of the program could be refined:

(1) The seedling assay is currently the most favored, but it can take several years to fully distinguish the different types of resistance. The development of chemical biomarkers or genomic tools for selecting for resistance would help increase our understanding of resistance and its genetic control.
(2) The recent development of microsatellite markers for POC has allowed a start on further investigation of genetic variation patterns across the range of the species. This work will complement previous isozyme and common garden studies and help demarcate potential additional areas for gene conservation.
(3) Research is needed to understand the evolutionary potential of *P. lateralis* and its potential impact on durability of resistance in POC. Investigations into the genetics and pathogenicity of isolates of *P. lateralis* from outside North America will expand our knowledge base.
(4) More work is needed to understand the limits to resistance in POC, particularly mortality and any fall down in resistance on the sites of highest risk: wet, low-lying areas.

Summary

Genetic variation within a species is the key to helping it evolve and adapt to changes in its environment, even to an unexpected threat such as a non-native pathogen. In an extreme case, such as the one that occurred with Port-Orford-cedar and the introduction of *P. lateralis*, humans can help re-establish a more balanced ecological equilibrium through active measures such as a resistance selection program. Such a program harnesses natural genetic variation within POC and would not have the negative side effects that other management activities could have. The program to develop *P. lateralis* resistance in POC has made significant progress in a relatively short period of time. Aspects of the program have involved not only USFS, BLM, and OSU, but also a wide array of other land managers. It is one of few operational resistance programs to non-native pathogens to produce significant levels of seed for potential restoration and reforestation. A large number of field selections have undergone the first rounds of resistance testing, breeding zones and a large genetic base has been established, seed orchard establishment is well underway, protocols for short-term resistance testing have been refined, field trials are underway, and the planting of resistant seedlings has started. Future efforts will focus on completing the development of first-cycle orchards, breeding to increase resistance and monitoring field trials for efficacy and durability of resistance. Genetic resistance is an invaluable tool to complement other management activities that prevent or reduce the spread of *P. lateralis*.

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