An overview of the Sudden Oak Death (SOD) disease caused by *Phytophthora ramorum*: Research Results and Challenges for the Pacific Northwest of North America

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Abstract

Sudden Oak Death (SOD), caused by the fungus-like pathogen *Phytophthora ramorum,* is a recently introduced plant disease killing oak and tanoak trees and causing foliar blight and shoot dieback on more than 100 plant species in North America and Europe. There are 14 California counties known to have Sudden Oak Death in the wild. In the Pacific Northwest (PNW) *P. ramorum* has been found in and near nurseries and eradicated. In Curry county, OR, *P. ramorum* is present in forests, where eradication and containment efforts have slowed its spread. It has also been found in several European countries in nurseries, gardens, and forested areas. *Phytophthora ramorum* has not been detected in the Southern hemisphere or in Asia. The disease is moved to new areas through the nursery trade and there is concern for spread to forests in the eastern US, where there are susceptible oak and understory species. It is important to prevent movement of *P. ramorum* in nursery stock. Research on biology and management of *P. ramorum* as well as a study of the potential risk to PNW forests is described. These research projects include a study of chemical fungicides on different life stages of the pathogen, testing of biocontrol products for use in controlling *P. ramorum* on foliage, examination of variability among isolates of *P. ramorum*, and screening of broadleaved trees and shrubs common in the PNW for susceptibility and sporulation potential of *P. ramorum* on foliage in order to evaluate the risk that this pathogen will become established in PNW forests.

Introduction

Phytophthora ramorum (Oomycetes: Peronosporales), the organism that causes Sudden Oak Death in North America and ramorum disease in Europe, causes damage on more than 100 species of trees and shrubs (USDA-APHIS 2012) from 36 different families. The organism thrives in wet conditions and spreads during periods of wet weather. Unlike most forest Phytophthoras that cause root disease, such as *P. cinnamomi* and *P. lateralis*, *P. ramorum* primarily attacks the above ground portions of the plant. The disease is named for the rapid decline and death experienced by hosts on which lethal stem cankers develop. Many of these hosts are in the Fagaceae, including oak (*Quercus* spp.), tanoak (*Notholithocarpus densiflorus*), and beech (*Fagus* spp.) (Table 1). Lethal stem cankers develop on larch (*Larix* spp.), a conifer host, which also supports prolific sporulation of the pathogen. Most other hosts develop leaf spots and/or twig dieback when infected by *P. ramorum*, and are not usually killed. These diseases are commonly referred to as ramorum blight or dieback. In North America, naturally infected hosts have been reported from forests and urban areas in coastal regions of California and southwestern Oregon. Since the organism is microscopic and symptoms resemble those of other plant pathogens or are minor on some hosts, a positive identification of *P. ramorum* requires the use of cultural and/or molecular diagnostic methods. *Phytophthora ramorum* is heterothallic, requiring two mating types for sexual recombination. There has been no evidence of this in the European and North American populations of *P. ramorum*, where population genetic studies have shown that reproduction is clonal (Ivors et al 2006). Based on molecular data there are four distinct clonal lineages of *P. ramorum* (Ivors et al. 2006; Grünwald et al. 2008b, Brasier 2012), one originally discovered in Europe, but also found in western North America (EU1), a new clade recently detected in Europe (EU2), and two only present in North America (NA1 and NA2).

Oak species in western North America

The oak species present in North America belong to the subgenus Quercus, sections Lepidobalanus (white oaks), Protobalanus (intermediate oaks), and Lobatae (red oaks). There are 13 species of Quercus native to California, as well as the closely related tanoak. Western North America is represented by three Level 1 ecoregions (CEC 1997). The southernmost ecoregion, containing central and northern California is ecoregion 11.0 (Figure 1), the Mediterranean California region, characterized by dry summers and wet winters. The climate tends to be moderate, with few temperature extremes. In northern California, Oregon, and Washington, coastal regions are in ecoregion 7.0 (Marine West Coast Forest) and inland areas are in ecoregion 6.0 (Northwestern Forested Mountains). The lower mainland portion of British Columbia is in ecoregion 7.0 and has the wettest climate.

Oak species occurring in coastal areas of California and southern Oregon where *P. ramorum* is present or is at risk of infesting, are Coast live oak (*Q. agrifolia*), Oregon white oak (*Q.*

garryana), California black oak (*Q. kelloggii*), Shreve's oak (*Q. parvula* var. *shrevei*), Canyon live oak (*Q. chrysolepis),* and tanoak (*N. densiflorus*). Other trees associated with oak are pines (*Pinus* spp.), Douglas-fir (*Pseudotsuga menziesii*), Pacific madrone (*Arbutus menziesii*), California bay laurel (*Umbellularia californica*), coast redwood (*Sequoia sempervirens*), and bigleaf maple (*Acer macrophyllum*).

The forest composition changes as one moves northward to the Pacific Northwest (PNW) region. The climate is wetter and coniferous species dominate. Oak species present in the PNW are limited to Oregon white oak, which extends as far north as Vancouver Island in British Columbia, and small amounts of California black oak, Canyon live oak, and tanoak in southern Oregon. Other oak species not native to the western US are present in ornamental landscapes, as street trees in urban areas, and in arboreta.

SOD – in CA/OR forests, Europe, risk to PNW forests

It is thought that *P. ramorum* was introduced to California forests via infected plants in the nursery trade from at least two locations (Mascheretti et al. 2008) in the mid 1990's. Due to the presence of susceptible hosts, mainly California bay laurel and tanoak, the disease spread rapidly and killed many thousands of trees. Disease spread in these forests is correlated with wet weather and presence of California bay laurel, on whose foliage *P. ramorum* produces abundant sporangia without killing the tree (Meentemeyer et al. 2004).

Tanoak is perhaps the most susceptible host for *P. ramorum*, as it can be killed by girdling stem cankers as well as produce inoculum on the foliage. This tree is in danger of being eliminated from the ecosystem in areas with high disease pressure. Other oak hosts, such as California black oak and Coast live oak, develop lethal stem cankers but are considered to be "dead end hosts", as the pathogen does not sporulate within these cankers and spread of the disease is halted. Recent studies have shown that some isolates of *P. ramorum* taken from oak cankers are less virulent than those taken from a sporulating host such as California bay laurel (Kasuga et al. 2012).

In Europe, *P. ramorum* has been present in the nursery trade since the early 1990s (Werres et al. 2001), and has become established in the UK on the invasive shrub *Rhododendron ponticum*. *Phytophthora ramorum* sporulates heavily on the foliage of *R. ponticum* and can spread to adjacent trees on which stem cankers are produced. In 2009 *P. ramorum* was found on Japanese larch (*Larix kaempferi*) in southwestern England. The pathogen produces large numbers of spores on the foliage of this host in addition to lethal stem cankers. Spores are produced in quantities sufficient to infect species that normally do not become infected in

North American forests, where the inoculum levels are lower. More than 3,000 ha of larch plantations have been felled since 2010 in an attempt to slow the spread of the disease (Forestry Commission 2012).

Forests in the PNW are at a lower risk for damage from *P. ramorum* based on current information about hosts and susceptibility and unfavorable environmental conditions in some areas. These forests are dominated by conifer species including Douglas-fir, Western hemlock (*Tsuga heterophylla*), and Sitka spruce (*Picea sitchensis*). All of these species are poor hosts for *P. ramorum* and natural infections on them are rare in California forests where *P. ramorum* is established. Western larch (*Larix occidentalis*) occurs in small quantities in coastal PNW forests, is somewhat susceptible to *P. ramorum,* and could potentially serve as an inoculum producing host. Hardwood species such as Pacific madrone and bigleaf maple, and understory Rhododendron (*R. macrophyllum*), salal (*Gaultheria shallon),* and Oregon grape (*Mahonia aquifolium*) also occur in PNW forests, but these are foliar hosts that produce inoculum at lower levels than California bay laurel and are lower risk for disease spread (Elliott and Chastagner, unpublished data).

<u>Consequences of SOD – nursery trade in eastern US and BC, Canada</u>

Long distance spread of *P. ramorum* occurs mainly by movement of infected nursery stock and some countries have imposed quarantines to reduce further spread (EPPO 2006). *Phytophthora ramorum* was first detected in a California nursery in 2001, and nurseries in CA, OR, WA, and BC in 2003. In 2004 a shipment of Camellias from a California nursery resulted in the spread of *P. ramorum* to nurseries across the US and in BC. Since then, infected ornamental nursery stock has been detected throughout the United States, as well as British Columbia, Canada. When *P. ramorum* is detected in a nursery, measures are taken to eradicate the pathogen. This can result in a financial burden on the nursery and some have gone out of business (Dart and Chastagner 2007).

In some cases *P. ramorum* is not completely eradicated from a nursery, and soils and water become contaminated. The pathogen has spread from nurseries to adjacent waterways in several locations in the PNW and southeastern US (Oak et al. 2012). Once *P. ramorum* is in a stream, it remains there. *Phytophthora ramorum* has spread from streams to vegetation in two locations. These sites were located outside of nurseries in WA and MS. Spread of *P. ramorum* from streams has not occurred in areas with forest infestations in CA and OR. Research is underway to determine the amount of *P. ramorum* inoculum in a stream needed to cause infection on plants, and the risk of spreading the disease in water.

Research Results – Biology and management of P. ramorum

In order to prevent outbreaks of *P. ramorum* in the forest, it is important to control it in nurseries. Methods that control the disease in soil and water have potential to prevent its movement from nurseries into landscapes, streams, and forests. Chemical and biological control methods can prevent infection of nursery stock (Chastagner and Hansen 2003, Elliott et al. 2009b). In the forest environment, prevention of spread by managing the sporulating host is one strategy being investigated. Research on the pathogen itself will assist in determining the risk of forest damage from *P. ramorum* should it become established outside of nurseries. These areas of research include population genetics, phenotypic variation, and host range. Some of these research results will be described here.

PCR-RFLP markers for differentiation of the North American and European lineages of *P. ramorum* populations

As more information about *P. ramorum* has accumulated, it has become clear that it is important to identify *P. ramorum* not only to the species level, but also to the clonal lineage and mating type level. A method was developed to identify which lineage an isolate of *P. ramorum* belongs to using PCR-RFLP of the mitochondrial Cox1 gene, first using the restriction enzyme ApoI to separate *P. ramorum* from other species and EU1 from North American populations, and AvaI to distinguish between NA1 and NA2 genotypes (Elliott et al. 2009d). These markers could be adapted for use in other assays, such as real-time PCR.

Phenotypic differences among isolates of *P. ramorum*

There are three major clonal lineages of *Phytophthora ramorum* present in North America and Europe (NA1, NA2, and EU1). Twenty-three isolates representing all three lineages were evaluated for phenotype including (i) aggressiveness on detached rhododendron leaves and (ii) growth rate at minimum, optimum, and maximum temperatures (Elliott et al. 2009c).

Isolates from the NA2 and EU1 lineages were the most aggressive on rhododendron foliage and isolates from the NA1 group were the least aggressive. NA1 isolates of *P. ramorum* were the most variable in aggressiveness and growth rate. This variability was due to the presence of non-wild type (nwt) isolates.

Phenotypic instability has been reported in the NA1 lineage, where “wild type” (wt) isolates having a uniform culture morphology and low variability in growth rate degenerate upon subculturing to become morphologically irregular and more variable in growth rate and pathogenicity (Brasier et al. 2006). Furthermore, differences in virulence can be seen in isolates of P. ramorum that are genetically similar but taken from different hosts (Huberli and Garbelotto 2012, Kasuga et al. 2012)

Susceptibility and sporulation potential of *P. ramorum* on broadleaf plant hosts in the Pacific Northwest

Susceptibility and sporulation on foliage of deciduous and evergreen broadleaf plant species were tested in June and August 2009 and 2010. For the initial screening, plant species were selected that are common in PNW forest and riparian areas including native and invasive species. California bay laurel (*Umbellularia californica*) was included as a standard for comparison, since this tree does not occur naturally in PNW forests but is important in spreading *P. ramorum* in California forests.

Average values of all variables were calculated (Table 3). These variables were standardized and agglomerative hierarchical cluster analysis (AHC) was performed. Four groups were identified using this method. Group 4, consisting only of California bay laurel, had the highest sporulation of any group. This suggests that none of the broadleaf hosts common in western Washington forests and riparian areas that were tested have the potential to be a sporulating host for *P. ramorum* similar to CA bay laurel. Asymptomatic infection frequency was highest in group 3, which consisted of both native and invasive species found in riparian areas. Principal components analysis (PCA) was performed on the standardized variables (Table 2).

In general, the results of this study indicate that PNW forests are not at high risk for damage caused by *P. ramorum*, based on the host plants tested. However, this is a subset of the many plant species that occur, and there may be a host species that is either extremely susceptible to infection or a prolific sporulator, that was not tested in this study. Plants posing the smallest risk of *P. ramorum* establishment were generally invasives and/or riparian species. The highest risk plants were commonly found in forested environments. These were fairly susceptible to infection and produced more chlamydospores than sporangia in their foliage.

In other systems, such as bay laurel in California, and *Rhododendron ponticum* and *Larix kaempferi* in the UK, *P. ramorum* outbreaks are driven by high concentrations of sporangia produced on foliage of these hosts. None of the PNW hosts tested produced as many sporangia as *U. californica*. Chlamydospore production was higher than sporangia production on many hosts in PNW forests that were examined in this study. Chlamydospores are a means by which *P. ramorum* can persist on a site in soil and decaying foliage, but will probably not produce large amounts of inoculum unless they germinate directly into sporangia, which can occur in flooded soils.

In a study of susceptibility of PNW conifer species to infection by *P. ramorum*, it was found that foliage of many hosts became infected when inoculated with a high concentration of zoospores in the spring, but later season foliage was less susceptible (Chastagner et al. 2012). Another project involved detailed studies of the infection of Douglas-fir by *P. ramorum* (McKeever 2010). Goals of this research included determining which tissues are colonized by the pathogen, whether woody tissues are able to support sporulation, the likelihood of stem infections occurring on Douglas-fir with intact bark, and the viability of the pathogen in foliage.

Screening of several fungicides for their effectiveness against *P. ramorum*

In this study eight chemicals with different modes of action were tested on fourteen isolates of *P. ramorum* representing the three major clonal lineages NA1, NA2, and EU1. The chemicals were tested for effectiveness against mycelial growth, chlamydospore production, and zoospore germination. In addition, Rhododendron 'Cunningham's White' plants were treated with fungicides and then challenged with *P. ramorum* to determine effectiveness of these treatments on host plants.

In the in-vitro tests, chlamydospore production increased, and then decreased after a certain dosage for some chemicals (Elliott et al. 2009a). The contact fungicides Manzate and Kocide both worked well on all life stages. Best results were obtained with Subdue Maxx on all life stages of *P. ramorum*, with the smallest dosage. However, other research has shown resistance developing in the EU population (Wagner et al. 2008). Furthermore, there is evidence for masking of symptoms on plants already infected with *P. ramorum* (Chastagner et al. 2008). Subdue Maxx has the advantage of being specific to Oomycetes, so beneficial fungi and bacteria are not affected, as with broad-spectrum chemicals such as Kocide and Manzate. Aliette was ineffective when tested with *P. ramorum* in vitro, and its mode of action may be related to increased plant defenses rather than direct effects against the pathogen.

Five of the fungicides were chosen for evaluation on plants. Three isolates of *P. ramorum*, one from each clonal lineage, were used in these tests. Infection frequency was greater than 90% on wounded leaves and less than 25% on unwounded leaves for the fungicides Manzate and Daconil, which was not significantly different from the untreated leaves. The most effective fungicides were Subdue Maxx and Acrobat. None of the unwounded leaves treated with the fungicide Reason became infected, and only 75% of the wounded leaves. Lesion area was largest on leaves treated with Manzate, Daconil, and untreated, and smallest on leaves treated with Acrobat, Reason, and Subdue Maxx.

Biological control of resprouting in tanoak and bay laurel using the fungus *Chondrostereum purpureum*

In southwest Oregon, an aggressive program of cutting and burning host plants in an effort to eradicate *P. ramorum* was instigated. In Fall 2009, field trials were established near Brookings, Oregon to assess the bioherbicidal efficacy of the fungus *Chondrostereum purpureum* (Chontrol™) on tanoak to inhibit resprouting, since these new sprouts are an inoculum reservoir. Treatment of stumps with *C. purpureum* has been shown to be effective for suppression of resprouting on several hardwood species, most notably red alder (*Alnus rubra*) (Becker et al. 2005; Wall 1990). Early results of field testing showed that *C. purpureum* was able to colonize the stumps of tanoak following treatment. Chontrol™ formulations appear to have some effect on reducing resprouting in tanoak, but the most effective and rapid treatment is the hack and squirt method of applying the herbicide Arsenal (imazapyr). Over time, applications of Chontrol™ may be a more permanent solution as the stumps become decayed. Stumps treated with Chontrol™ formulations with and without inoculum had more dead sprouts than in the Garlon (triclopyr) spray treatment. With incomplete coverage of herbicide, fewer and healthier sprouts formed than with an application of Chontrol™. Laboratory testing of three California isolates of *C. purpureum* indicate that the fungus can colonize bay laurel stems, and further testing under natural conditions is planned. If a formulated product of *C. purpureum* and/or its mixture with other stem and wood decay fungi applied to tanoak and bay laurel does inhibit the trees from growing new sprouts, this *P. ramorum* inoculum reservoir would be reduced or eliminated in the ecosystem, providing an alternative to chemical herbicides in areas where their application is not prudent or permitted.

Some Challenges for the Pacific Northwest region of North America:

● Further effort to search for potential "spore pump" hosts is needed, as such hosts are thought to be necessary for *P. ramorum* to inflict substantial damage to PNW forest ecosystems and the nursery industry. This should include continued research on screening of conifer species for their susceptibility to infection and sporulation potential of *P. ramorum*.

● The economic impact of SOD on nursery and forest industries. For example, the value of the log exports at risk (in BC, $580 million), is almost 30 times larger than the value of high risk horticultural imports (about $20 million). It seems sensible to advocate that more should be done to limit risky horticultural imports.

● Climate change. Increased precipitation during spring is likely to be associated with greater frequency of *P. ramorum* in areas where it already occurs and expansion of the pathogen to new locations. Continued warming in areas with sufficient moisture would increase suitable climate for *Phytophthora* spp., resulting in increased tree mortality if the pathogen is introduced to those areas. These changes in climate may increase damage to PNW forest ecosystems from native *Phytophthora* spp. (e.g., *P. quercina*), invasive alien *Phytophthora* spp. (e.g., *P. cinnamomi* and *P. lateralis*), and other emerging *Phytophthora* spp.

● The emergence of a new (EU2) lineage of *P. ramorum* in the UK and its potential threat to PNW forest ecosystems and nursery industry needs to be examined.

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Table 1. Susceptibility of various oak species to bole infection by *Phytophthora ramorum*.

Species	Common name	Location	*P. ramorum* host	Reference
Subgenus Quercus				
Section Lepidobalanus - White oaks				
Quercus douglasii	Blue oak	California	Less susceptible*	Rizzo et al 2002
Q. garryana	Oregon white oak	Western North America	Less susceptible	Hansen et al. 2005
Q. lobata	Valley oak	California	Less susceptible	Rizzo et al 2002
Q. faginea	Portuguese Oak	Southwestern Europe	Highly susceptible	Moralejo et al. 2009
Q. ilex	Holly Oak or Holm Oak	Southern Europe, northwestern Africa	Moderately susceptible, regulated	Moralejo et al. 2009, Brasier et al. 2002
Q. pubescens	Downy Oak	Europe, Anatolia	Highly susceptible	Moralejo et al. 2009
Q. petraea	Sessile oak	Europe	Bole host, associated#	USDA APHIS 2012
Q. robur	Pedunculate Oak	Europe, West Asia	Less susceptible	Brasier et al. 2002
Section Protobalanus – Intermediate oaks				
Q. chrysolepis	Canyon live oak	California	Less susceptible, regulated	Murphy and Rizzo 2003, Hansen et al. 2005
Section Mesobalanus				
Q. canariensis	Mirbeck's Oak or Algerian Oak	North Africa & Spain	Highly susceptible	Moralejo et al. 2009
Q. pyrenaica	Pyrenean Oak	southwestern Europe	Highly susceptible	Moralejo et al. 2009
Section Lobatae – Red oaks				
Q. agrifolia	Coast live oak	California	Bole host, regulated	Rizzo et al. 2002
Q. kelloggii	California black oak	California	Moderately susceptible, regulated	Rizzo et al. 2002, Hansen et al. 2005
Q. parvula var. shrevi	Shreve's oak	California	Bole host, regulated	USDA APHIS 2012
Q. falcata	Southern red oak	SE North America	Highly susceptible, regulated	Brasier et al. 2004
Q. palustris	Pin oak	Eastern North America	Highly susceptible	Rizzo et al. 2002
Q. rubra	Northern red oak	Europe, Eastern North America	Moderately susceptible, associated	Brasier et al. 2002, Rizzo et al. 2002
Section Cerris				
Q. cerris	European turkey oak	Southern Europe, SW Asia	Susceptible, regulated	Brasier et al. 2002
Q. suber	Cork Oak	Southwestern Europe, northwestern Africa	Moderately susceptible	Moralejo et al. 2009, Brasier et al. 2002
Subgenus Cyclobalanopsis				
Q. acuta	Japanese evergreen oak	Japan, Korea	Bole host, associated	USDA APHIS 2012

*Susceptibility in lab tests using bole infection and log inoculations. #Associated – regulated as nursery stock

Table 2. Results of principal components analysis of foliar susceptibility and sporulation data collected from broadleaved plants in the Pacific Northwest inoculated with Phytophthora ramorum.

Factor	% of variation	Description
F1	36.16	Sporulation (sporangia/ml, chlamydospores/ml)
F2	32.13	Susceptibility (visible infection frequency, lesion area)
F3	14.73	Asymptomatic infection frequency

Table 3. Broadleaf plants tested for susceptibility and sporulation potential of *Phytophthora ramorum* in June and August, 2009 and 2010. Average values for all treatments and sampling times are shown for each variable. Sporulation potential is shown by number of sporangia or chlamydospores per ml of suspension. AHC group = groups obtained by hierarchical cluster analysis, F1 + F2 = sum of two largest principal components.

Common name	Scientific name	Symbol	Visible infection frequency	Lesion area, mm^2	Asymptomatic infection frequency	Sporangia	Chlamydospores	AHC group	F1 + F2
California bay laurel	*Umbellularia californica*	UMCA	0.58	217	0.10	60	160	4	3.16
Bigleaf maple	*Acer macrophyllum*	ACMA	0.75	1240	0.08	33	52	1	3.05
Pacific madrone	*Arbutus menziesii*	ARME	0.50	2798	0.15	4	33	1	1.98
Wood rose	*Rosa gymnocarpa*	ROGY	0.88	322	0.10	10	32	1	1.66
Vine maple	*Acer circinatum*	ACCI	0.83	372	0.10	15	15	1	1.54
Pacific dogwood	*Cornus nuttallii*	CONU	0.43	1734	0.10	9	18	1	1.16
Pacific rhododendron	*Rhododendron macrophyllum*	RHMA	0.48	1072	0.03	2	35	2	1.16
Garry oak	*Quercus garryana*	QUGA	0.60	331	0.20	18	66	2	0.62
English laurel	*Prunus laurocerasus*	PRLA	0.38	841	0.08	3	68	2	0.60

Common name	Scientific name	Symbol	Visible infection frequency	Lesion area, mm^2	Asymptomatic infection frequency	Sporangia	Chlamydospores	AHC group	F1 + F2
Salal	*Gautheria shallon*	GASH	0.43	127	0.10	5	84	2	0.19
Oregon grape	*Mahonia aquifolium*	MAAQ	0.18	262	0.18	14	106	2	-0.55
Red osier dogwood	*Cornus sericea*	COSE	0.33	63	0.13	8	35	2	-0.67
English ivy	*Hedera helix*	HEHE	0.01	1	0.03	16	40	2	-0.91
Snowberry	*Symphoricarpos albus*	SYAL	0.28	84	0.30	21	41	3	-1.44
Scouler willow	*Salix scouleriana*	SASC	0.13	18	0.10	5	8	2	-1.53
Japanese knotweed	*Polygonum cuspidatum*	POCU	0.25	707	0.28	6	9	3	-1.56
Himalayan blackberry	*Rubus armeniacus*	RUAR	0.05	35	0.25	6	36	3	-2.47
English holly	*Ilex aquifolium*	ILAQ	0.01	107	0.30	10	73	3	-2.47
Red alder	*Alnus rubra*	ALRU	0.23	97	0.55	13	25	3	-3.53

Figure 1. Map of ecoregions in Western North America (CEC 1997). The Pacific Northwest (PNW) has several descriptions but for the purpose of this article it is composed of regions of northern California, Oregon, Washington, and British Columbia west of the Cascade Mountains.