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Allozyme Variation of Port-Orford-Cedar (*Chamaecyparis lawsoniana*): Implications for Genetic Conservation

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ABSTRACT. Variation at 32 allozyme loci in nine disjunct populations of Port-Orford-cedar (POC) from the California floristic region was measured to estimate the amount and pattern of genetic variability in natural stands. Variation in electrophoretically detectable loci was moderately high, with mean number of alleles per locus = 1.9, 64.9% polymorphic loci, and observed heterozygosity = 0.13. Diversity was highest in the seven populations from the coastal mountains and lowest in the two populations from the inland portion of POC's distribution. The Sacramento River population in the inland group had only 44% polymorphic loci, and observed heterozygosity equaled 0.05. Populations in the inland region were allozymically distinct from those in the coastal region as well as from each other. Mean genetic distances among the coastal populations were 0.005 compared to 0.016 between the inland and coastal groups and 0.013 between inland populations. Population variation accounted for 5% of the total allozyme diversity. Genetic conservation efforts for POC in California are evaluated. In situ areas are already being established in some genetically important localities, although many gaps remain; ex situ coverage is inadequate. FOR. SCI. 37(4):1060–1077.

ADDITIONAL KEY WORDS. *Phytophthora lateralis*, genetic diversity, isozymes.

THREATS TO DIVERSITY OCCUR AT MANY LEVELS of biological organization, from genes to species to ecosystems. Although conservation biologists have focused primarily on preserving rare and endangered species, they are increasingly recognizing the vulnerability of genetic variation within widespread species and the need for conserving intraspecific structure (Schonewald-Cox et al. 1983, Falk and Holsinger 1991). Whether a specific program for genetic conservation is undertaken, or genetic concerns are included in a general management plan, knowledge of genetic variation in the species of concern is important for effective genetic conservation. This paper reports a small study of genetic variation in populations of Port-Orford-cedar (*Chamaecyparis lawsoniana*) in the California floristic region and discusses implications for its genetic conservation.

Port-Orford-cedar (POC) is restricted to northwestern California (Figure 1) and southwestern Oregon where it grows naturally in disjunct populations on sites that have abundant soil moisture throughout the year (Zobel et al. 1985). In California it grows commonly on ultramafic soils, where competition from other species is reduced. Despite its limited distribution, POC is highly valued as a commercial timber species, especially in the Japanese export market, where it is sold as a

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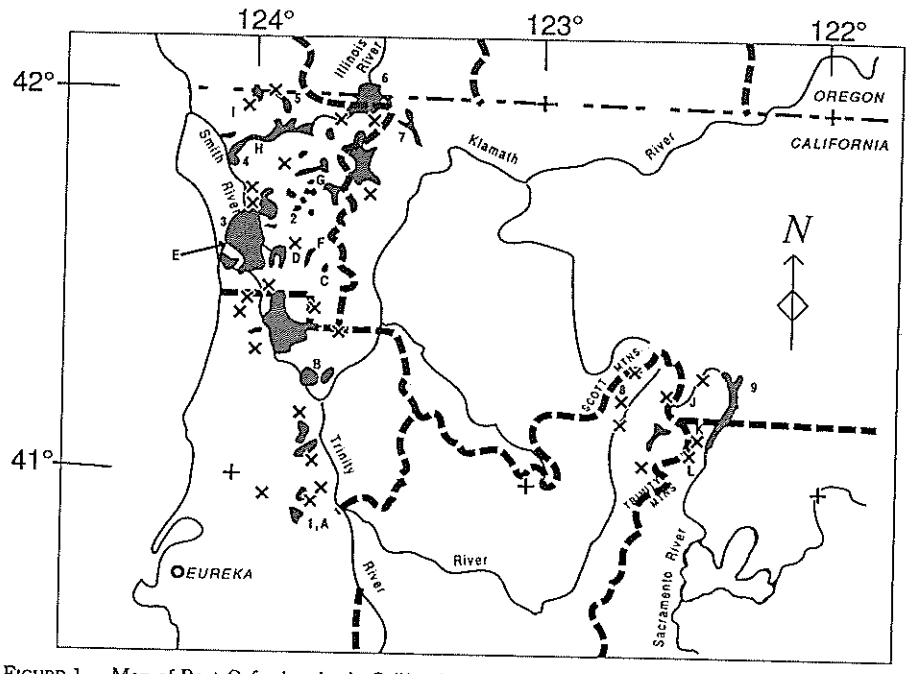

FIGURE 1. Map of Port-Orford-cedar in California and southern Oregon showing natural distribution (solid areas and crosses) (after Griffin and Critchfield 1976), locations of collection stands (marked by numbers), and proposed and established reserves containing Port-Orford-cedar (marked by letters). Collection stands: 1 = Horse Mtn., 2 = Ship Mtn., 3 = Smith River, 4 = Allen Gulch, 5 = Shelly Creek, 6 = Elder Creek, Oregon, 7 = Indian Creek, 8 = Trinity River, 9 = Sacramento River. Reserves: A = Horse Mtn. Bot. Area, B. = Adorni Research Natural Area (RNA), C = Rock Creek Butte RNA, D = Smith River Wild River, E = Upper Goose Creek RNA, F = Siskiyou Wilderness, G = Bear Basin Bot. Area, H = Craigs Creek RNA, I = Horton RNA, J = Cedar Basin RNA, K = Castle Crags Wilderness, L = Castle Crags State Park.

replacement for depleted native hinoki (*C. obtusa,* Cohn 1986). The value of POC wood has steadily increased, and the highest quality logs have commanded prices up to $6000/mbf (Zobel et al. 1985).

Over the past several decades, POC has been threatened in nurseries, ornamental plantings, and its native range by a fatal root disease caused by *Phytophthora lateralis.* The disease, specific to POC, was first found in 1923 in a nursery in British Columbia, Canada, and has spread rapidly through native stands since its first documented occurrence in the wild in 1952. Fungal spores are dispersed through a drainage with flowing water. Another spore type is moved uphill and between drainages in mud. The movement of mud on vehicles and logging equipment is a major mechanism of disease spread (Zobel et al. 1985). Only a few major drainages in California remain uninfested, including a disjunct set of inland populations in the Scott and Trinity Mountains of California (USDA Forest Service 1980). There appears to be little genetic resistance to the root rot (Zobel et al. 1985), and mortality in infested stands is high.

Little is known about the patterns of genetic variation in natural forests of POC. Observations of water resistance of leaves (Zobel and Liu 1980) and bud phenology (Zobel 1983) showed little variation among geographic sources or individual trees grown in a common environment, suggesting low levels of variability for at

least some traits. In horticultural types, however, POC is highly variable. Over 220 cultivars have been described, more than for any other conifer (Rouane 1973).

METHODS

Sample Populations

Nine stands were sampled, including seven from the northwestern coast ranges and two from the disjunct Scott and Trinity Mountains (Table 1). With one exception, all stands were in California. All stands were on soils of ultramafic origin. These populations included extremes for the species in elevation, longitude, and latitude in the California floristic region, as well as in degree of fungal infection. The seven "coastal" stands included Horse Mountain (1380 m), at the southernmost extent of POC's range in the lower Trinity River drainage; Ship Mountain (1015 m), Smith River (150 m), Allen Gulch (460 m), and Shelly Creek (800 m) in the Smith River drainage; Elder Creek, Oregon (1290 m) in the Illinois River drainage just across the state border; and Indian Creek (1230 m) in the Klamath River drainage. The two "inland" stands included the Trinity River (1015 m) in the upper Trinity River drainage, and the Sacramento River (1380–1700 m) in the upper Sacramento River drainage. The Allen Gulch stand was the most severely infested with *Phytophthora,* while the Horse Mountain, Indian Creek, Trinity River, and Sacramento River stands were apparently uninfested (Table 2).

Ripe cones were collected from low to mid crowns of 20 trees in each stand. Trees in a stand were separated by at least 30 m. Sufficient cones were collected to provide seeds for immediate research as well as to establish a small germplasm collection for POC.

Electrophoretic Methods

Extracted seeds were stratified in cold moist conditions for 30 days and germinated at 21°C in an incubator until radicles emerged about 1 cm (within 7 days). Five to eight megagametophytes per tree were subjected to starch gel electrophoresis following methods of Conkle et al. (1982) and Millar (1985) with minor modifications. Thirty-two loci resolved from the following 19 enzymes: (1) alanine aminopeptidase (ALA), (2) aldolase (ALD), (3) catalase (CAT), (4) fluorescent esterase (FES), (5) fructose diphosphatase (FDP), (6) glutamate oxaloacetate-transaminase (GOT), (7) glutamate dehydrogenase (GDH), (8) glucose-6-phosphate dehydrogenase (G6P), (9) glyceraldehyde-3-phosphate dehydrogenase (G3P), (10) isocitrate dehydrogenase (IDH), (11) leucine aminopeptidase (LAP), (12) malate dehydrogenase (MDH), (13) menadione reductase (MNR), (14) mannose phosphate isomerase (MPI), (15) peptidase (PEP), (16) phosphoglucomutase (PGM), (17) phosphoglucose isomerase (PGI), (18) 6-phosphogluconic dehydrogenase (6PG), (19) UDG-glucose pyrophosphatase (UGP). Loci were numbered with the lowest value representing the most anodally migrating locus. Diploid genotypes of sampled trees were determined at a minimum probability of 0.06 of misclassifying a heterozygote as a homozygote (Morris and Spieth 1978).

TABLE 1.

Allozyme frequencies in nine populations of Port-Orford-cedar in California.

Locus/ allele[b]	Populations[a]								
	Coastal							Inland	
	HM	SM	SmR	AG	SC	EC	IC	TR	SaR
	Sample size—mean number of haploid genotypes sampled per locus								
	39	33	30	31	39	31	31	29	29
*Ala*1									
1	0.950	0.882	0.933	0.929	0.925	0.882	0.889	0.955	1.000
2		0.059	0.067	0.036	0.025			0.045	
3	0.050	0.059		0.036	0.050	0.118	0.111		
*Ald*1									
1	0.950	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
2	0.050								
*Ald*2									
1	0.975	0.808	1.000	0.750	0.800	1.000	0.722	1.000	0.964
2	0.025	0.192		0.250	0.175		0.222		
3					0.025		0.056		0.036
*Cat*1									
1	0.875	0.853	0.824	0.955	0.825	0.912	1.000	0.950	0.964
2	0.125	0.147	0.147	0.045	0.125	0.059		0.050	0.036
3					0.025				
4					0.025				
5			0.029			0.029			
*Fes*1									
1	0.825	0.906	0.971	0.833	0.925	0.937	0.722	0.929	1.000
2	0.175	0.063		0.083	0.050	0.063	0.167		
3		0.031					0.111		
4			0.029	0.083	0.025			0.071	

TABLE 1. Continued.

Fes2							:		
1	1.000	1.000	0.964	1.000	1.000	1.000	1.000	1.000	1.000
2			0.036				:		
Fdp1							:	1.000	0.964
1	0.600	0.882	0.937	0.893	0.775	0.971	0.833		0.036
2	0.400	0.118	0.063	0.107	0.125	0.029	0.167	:	
3					0.100			:	
Fdp2							:	1.000	1.000
1	1.000	1.000	1.000	1.000	0.925	0.971	0.944	:	
2					0.075	0.029	0.056	:	
3									
Got1							:	1.000	1.000
1	0.975	1.000	1.000	0.964	1.000	1.000	1.000	:	
2	0.025			0.036				:	
3									
Got2							:	0.846	1.000
1	0.900	0.676	0.912	0.964	0.850	0.971	0.833	:	0.154
2	0.050	0.118	0.088		0.050	0.029	0.111	:	
3	0.025	0.206			0.100		0.056	:	
4				0.036				:	
5	0.025							:	
Gdh1							:	0.687	0.929
1	0.925	0.875	0.937	0.821	0.925	0.941	0.722	:	0.250 0.071
2	0.050	0.094	0.031	0.179	0.075	0.059	0.278	:	0.063
3	0.025	0.031	0.031					:	

Locus/ allele[b]	Populations[a]								
				Coastal				Inland	
	HM	SM	SmR	AG	SC	EC	IC	TR	SaR
*G6p*1									
1	0.875	0.906	0.967	0.917	0.800	0.781	0.889	0.929	0.929
2	0.075	0.031	0.033	0.083	0.125	0.156	0.111	0.071	0.036
3	0.025	0.063			0.050	0.031			
4					0.025	0.031			
5	0.025								
*G3p*1									
1	1.000	1.000	1.000	1.000	0.944	1.000	1.000	1.000	1.000
2					0.056				
*Idh*1									
1	0.975	0.937	0.969	0.923	0.800	0.765	0.944	1.000	0.929
2		0.063	0.031	0.038	0.100	0.235	0.056		
3					0.075				
4				0.038	0.025				
5	0.025								
*Lap*1									
1	0.975	0.971	1.000	0.962	0.925	0.941	1.000	0.955	0.893
2	0.025	0.029		0.038	0.075	0.059		0.045	0.107
3									
*Mdh*1									
1	0.900	1.000	0.937	0.846	0.775	0.971	0.944	1.000	1.000
2	0.100		0.063	0.154	0.225	0.029	0.056		

TABLE 1. Continued.

Mdh2										
1	0.800	0.971	0.844	0.929	0.775	0.971	0.944	:	1.000	1.000
2	0.125		0.063		0.025			:		
3	0.050		0.063	0.036	0.125		0.056	:		
4	0.025	0.029	0.031		0.075	0.029		:		
5				0.036				:		
Mdh3										
1	0.975	0.765	0.941	0.893	0.775	0.941	1.000	:	0.950	1.000
2	0.025	0.235	0.059	0.107	0.225	0.059		:	0.050	
Mdh4										
1	0.941	1.000	1.000	1.000	1.000	1.000	1.000	:	1.000	1.000
2	0.059							:		
Mnr1										
1	1.000	1.000	1.000	1.000	0.972	1.000	0.944	:	1.000	1.000
2					0.028		0.056	:		
Mnr2										
1	0.947	1.000	1.000	0.962	1.000	0.969	1.000	:	0.778	1.000
2	0.053			0.038				:	0.222	
3						0.031		:		
Mpi1										
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000	:	0.800	1.000
2								:	0.200	
Pep1										
1	0.925	0.929	0.781	0.885	0.850	0.875	0.812	:	0.650	0.500
2	0.075	0.071	0.187	0.115	0.150	0.125	0.187	:	0.350	0.500
3			0.031					:		
Pep2										
1	0.975	0.971	0.969	0.857	0.975	0.912	1.000	:	1.000	1.000
2	0.025	0.029	0.031	0.143	0.025	0.059		:		

Locus/ allele[b]	Populations[a]									
	Coastal							:	Inland	
	HM	SM	SmR	AG	SC	EC	IC	:	TR	SaR
3						0.029		:		
*Pgm*1										
1	0.825	0.625	0.719	0.769	0.650	0.588	0.722	:	0.562	0.786
2		0.125	0.125		0.025			:	0.375	0.107
3	0.150	0.063	0.125	0.077	0.250		0.222	:		
4	0.025	0.187		0.154	0.075	0.294	0.056	:	0.063	0.107
5			0.031			0.118		:		
*Pgi*1										
1	0.950	0.882	1.000	0.929	0.925	0.941	1.000	:	1.000	1.000
2	0.025	0.088						:		
3	0.025	0.029				0.029		:		
4					0.075	0.029		:		
5				0.071				:		
*Pgi*2										
1	0.575	0.647	0.706	0.821	0.800	0.618	0.833	:	0.500	0.393
2	0.275	0.353	0.265	0.179	0.200	0.382	0.167	:	0.500	0.607
3	0.025							:		
4	0.125		0.029					:		

TABLE 1. Continued.

6Pg1										
1	0.825	0.781	0.933	0.583	0.800	0.853	0.778	:	0.950	0.786
2	0.150	0.187	0.067	0.417	0.200	0.147	0.222	:	0.050	0.143
3		0.031						:		0.071
4	0.025							:		
6Pg2										
1	0.975	1.000	1.000	0.834	0.950	1.000	1.000	:	1.000	1.000
2	0.025			0.167				:		
3					0.050			:		
Ugp1										
1	0.921	0.857	0.933	0.929	0.750	0.818	0.722	:	0.667	0.792
2	0.053	0.143	0.067	0.036	0.225	0.182	0.278	:	0.333	
3	0.026				0.025			:		
4				0.036				:		0.208
Ugp2										
1	1.000	0.906	0.906	0.917	0.900	0.969	0.889	:	0.889	0.929
2		0.094	0.094	0.083	0.100	0.031	0.056	:	0.111	0.071
3							0.056	:		
Ugp3										
1	0.950	0.824	0.875	1.000	0.875	0.912	1.000	:	1.000	0.571
2	0.025	0.118	0.063		0.125	0.059		:		0.429
3	0.025	0.059	0.063			0.029		:		

[a] *HM* = Horse Mtn., *SM* = Ship Mtn., *SmR* = Smith River, *AG* = Allen Gulch, *SC* = Shelly Creek, *EC* = Elder Creek, *IC* = Indian Creek, *TR* = Trinity River, *SaR* = Sacramento River.

[b] Loci, and alleles within loci, are numbered with the lowest value being the most anodally migrating.

Analysis

Allele frequencies for each population were calculated from the inferred diploid genotypes of the sample trees. Observed and expected heterozygosities, hierarchical diversity statistics (Nei 1973), Nei's (1978) unbiased genetic distance measures, and unweighted-pair-group-method algorithm (UPGMA) cluster analyses (Sneath and Sokal 1973) were calculated from allele frequencies with the BIOSYS-1 computer program (Swofford and Selander 1981).

RESULTS

Relative to other conifers, POC in the California floristic region is moderately variable in allozymes (Table 1). All 32 loci varied in at least one population, although several loci were monomorphic in most populations (*Fes*2, *Ald*1, *Got*1, *G3p*1, *Mdh*4, *Mdh*5, *Mpi*1). Differences in allele frequencies distinguished the two inland populations from the seven coastal populations of POC in California (Table 1). The inland populations were much more monomorphic and, in polymorphic loci, had higher frequencies of common alleles than the coastal populations. Differences in frequency of common alleles between the coastal and at least one inland population were in *Gdh*1, *Lap*1, *Pep*1, *Pgm*1, *Pgi*2, *Ugp*1, and *Ugp*3. Few alleles were unique to the inland group at these loci, but the patterns of allele frequencies among alleles at a locus differed between the coastal and inland groups (e.g., *Pgm*1). In the case of *Pgi*2, the rank of common alleles was reversed.

The percent of loci polymorphic in the inland populations was about half that of the most variable coastal population (Shelly Creek) (Table 2). The Sacramento River population was especially low in variability, with observed heterozygosity (0.05) about one-quarter that of the most variable population (Shelly Creek) in the whole study. The ratio of observed to expected heterozygosity was also low in the Sacramento River population (0.46), about half the ratio in the other populations. Many loci (*Ala*1, *Ald*2, *Fes*1, *Fdp*1, *Got*2, *Idh*1, *Mdh*1, *Mdh*2, *Mdh*3, *Pep*2, *Pgi*1, *Ugp*3) that were polymorphic in most coastal populations were monomorphic in at least one of the two inland populations (Table 1). The Sacramento River and Trinity River populations each had only two-thirds of the total number of alleles as the most variable population sampled (Table 2).

Large differences in allele frequencies also occurred between the two populations in the inland group. The Sacramento River population had fewer alleles and was more monomorphic than the Trinity River population at some loci, while the reverse was true for other loci. This pattern occurred at 10 loci (*Ala*1, *Ald*2, *Fes*1, *Fdp*1, *Got*2, *Idh*1, *Mdh*3, *Mnr*2, *Mpi*1, *Ugp*3).

Of the coastal populations, the Indian Creek population resembled the inland populations in being monomorphic at two (*Pep*2, *Pgi*1) of the four loci that were monomorphic in the inland populations but polymorphic in most of the coastal populations. The Shelly Creek and Horse Mountain populations had the highest total and mean number of alleles per locus and highest percent of polymorphic loci (Table 2). The Horse Mountain stand also had an unusually high number (8) of unique alleles. The Shelly Creek population had the highest observed heterozygosity.

TABLE 2.

Genetic variability measures at 32 loci in 9 populations of Port-Orford-cedar in California.

Population	Total no. alleles	No. unique alleles	Mean no. alleles	% of loci polymorphic[e]	Observed heterozygosity	H_o/H_e
Coastal populations:						
Indian Cr.[d]	56	2	1.7	56.2	0.15	0.98
Smith River[b]	61	2	1.9	62.5	0.11	0.95
Ship Mtn.[b]	63	0	2.0	65.6	0.14	0.83
Elder Cr.[c]	62	1	1.9	71.9	0.13	0.99
Allen Gulch[a]	61	4	1.9	75.0	0.13	0.83
Horse Mtn.[d]	72	8	2.2	78.1	0.11	0.74
Shelly Cr.[a]	72	3	2.3	81.2	0.19	0.93
Mean	74	3	2.0	70.1	0.14	0.89
Inland populations:						
Sac. River[d]	49	0	1.5	43.7	0.05	0.46
Trinity River[d]	50	2	1.6	50.0	0.12	0.84
Mean	50	1	1.5	46.9	0.08	0.67
OVERALL MEAN	61	2	1.9	64.9	0.13	0.85

[a–d] Degree of fungal infestation, *a* = severe, *d* = apparently uninfested.
[e] Loci with more than one allele.

Genetic distance (Table 3) and cluster analyses (Figure 2) summarize regional and population differences for all loci. The average genetic distance between the coastal and inland groups was 0.016, three times the average distance among populations within the coastal group. Genetic distances clearly separated the inland group from the coastal group and also the two inland populations from each other (Figure 2). On average, 5% of the total allozyme diversity was attributable to differences among populations, the remainder being attributable to within-population diversity.

DISCUSSION

VARIATION

Despite its patchy distribution, POC in the California floristic region has moderately high levels of allozyme variability within stands. Expected heterozygosity in POC is similar to the values for other California conifers that have small to moderate-sized distributions, including Monterey pine (*Pinus radiata*), bishop pine (*P. muricata*), knobcone pine (*P. attenuata*) (Millar et al. 1988), Monterey cypress (*Cupressus macrocarpa*) (Conkle 1987), and giant sequoia (*Sequoiadendron giganteum*) (Fins and Libby 1982) (Table 4). Variability in POC is considerably lower, however, than in California populations of widespread western conifers, such as ponderosa pine (*Pinus ponderosa*) (Conkle and Westfall 1983), Jeffrey pine (*P. jeffreyi*) (Conkle 1981, Furnier and Adams 1986), sugar pine (*P. lambertiana*) (Conkle 1981), and Douglas-fir (*Pseudotsuga menziesii*) (Conkle 1981). Compared to California populations of other species in the *Cupressaceae,*

TABLE 3.

Genetic distances among populations of California Port-Orford-cedar. Nei's (1978) unbiased genetic distances among individual populations are above the diagonal; averages are below diagonal.

Populations[a]	HM	SM	SmR	AG	SC	EC	IC	:	TR	SaR
Coastal populations:										
Horse Mtn.	—	0.008	0.004	0.009	0.007	0.009	0.006	:	0.019	0.021
Ship Mtn.		—	0.003	0.006	0.003	0.004	0.004	:	0.011	0.017
Smith River			—	0.007	0.004	0.004	0.006	:	0.008	0.012
Allen Gulch				—	0.004	0.008	0.001	:	0.020	0.023
Shelly Cr.		0.005			—	0.006	0.002	:	0.018	0.022
Elder Cr.						—	0.007	:	0.010	0.014
Indian Cr.							—	:	0.010	0.022
Inland populations:										
Trinity River		0.016						:	—	0.013
Sacramento River								:	0.013	—

[a] HM = Horse Mountain, SM = Ship Mountain, SmR = Smith River, AG = Allen Gulch, SC = Shelly Creek, EC = Elder Creek, IC = Indian Creek, TR = Trinity River, SaR = Sacramento River.

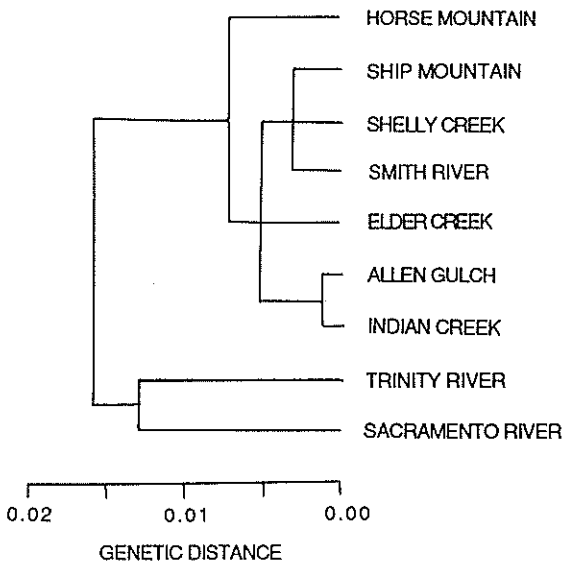

FIGURE 2. Phenogram for California Port-Orford-cedar populations. Clusters are produced using the unweighted-pair-group-method algorithm (UPGMA) with Nei's (1978) unbiased genetic distances.

POC has higher variability than western redcedar (*Thuja plicata*) (Copes 1981) and lower variability than incense-cedar (*Calocedrus decurrens*) (Harry 1984), but is similar to the 11 cypress species native to the California floristic region (Conkle 1987, Millar unpub. data) (Table 4).

TABLE 4.

Measures of allozyme diversity for some western conifer species that grow in California.

Species	No. alleles/locus	% loci polymorphic	Expected heterozygosity	References
Thuja plicata	1.0	0	0.00	Copes 1981
Pinus torreyana	1.0	3	0.00	Ledig and Conkle 1983
Pinus muricata	1.6	47	0.12	Millar et al. 1988
Pinus attenuata	1.7	55	0.13	Millar et al. 1988
Sequoiadendron giganteum	1.5	50	0.14	Fins and Libby 1982
Pinus radiata	1.9	58	0.14	Millar et al. 1988
Chamaecyparis lawsoniana	1.9	65	0.15	current paper
Cupressus macrocarpa	1.2	61	0.18	Conkle 1987
Calocedrus decurrens	2.5	50	0.18	Harry 1984
Pinus lambertiana	2.8	80	0.28	Conkle 1981
Pinus contorta	2.7	89	0.19	Conkle 1981
Pinus jeffreyi	2.9	86	0.26	Conkle 1981, Furnier and Adams 1986
Pinus ponderosa	3.0	89	0.21	Conkle and Westfall 1983
Pseudotsuga menziesii	3.9	74	0.33	Conkle 1981

Abundant fossil evidence indicates that POC had a wide distribution in North America during the Tertiary (Edwards 1983). The diverse associates of POC in these fossil floras suggest that POC grew in many habitats and climates. The limiting factor for POC then and now appears to be soil moisture (Zobel et al. 1985, Edwards 1985). Humid climates with wet summers were common throughout western North America until the late Tertiary, when long summer droughts, typical of present conditions in western North America, developed. This climatic change apparently triggered widespread extinction of POC populations and the expansion of other conifers, especially Douglas-fir, that tolerate high water stress. Port-Orford-cedar survived in northwestern California and southwestern Oregon where soil moisture remained adequate throughout the year for its growth. Within this region, extensive ultramafic soils support POC growth. These soils retain high moisture levels that are important for POC, and their extreme nutrient levels exclude competitors such as Douglas-fir. Port-Orford-cedar, like other California members of the *Cupressaceae* including incense-cedar, Sargent cypress (*Cupressus sargentii*), MacNab cypress (*C. macnabiana*), and common juniper (*Juniperus communis*), tolerates the chemical conditions of ultramafic soils, and these sites have become refugia for POC (Raven and Axelrod 1978, Kruckeberg 1984).

Despite the current distribution of POC in scattered, small stands, none of the coastal populations we studied showed evidence of being founded by a few colonizers or having undergone prolonged reductions in size. Similar high levels of ancestral variability have been retained in small, isolated populations of *Cupressus* (Conkle 1987) and in several small mainland and island populations of bishop, knobcone, and Monterey pines (Millar et al. 1988). The inland populations, by contrast, with only half the variability and higher homozygosity of the most diverse coastal populations, apparently experienced either past bottlenecks or strong selection.

Although allozyme variability within the small, disjunct stands of POC is moderately high, differentiation among stands is relatively low. For other related conifers in California that have similar distribution patterns, population differentiation of allozymes is greater. In Monterey cypress (Conkle, 1987), in the other ten cypress species native to the California floristic region (Millar unpub. data), and in giant sequoia (Fins and Libby 1982), average population differentiation within species was 10–15% of the total diversity. By contrast, differences among populations in Sierra Nevadan incense-cedar accounted for only 4% of the total allozyme diversity (Harry 1984). Incense-cedar in the Sierra Nevada, unlike the cypresses, giant sequoia, and POC, grows in large continuous populations where there is ample opportunity for gene flow to counter the effects of genetic drift. The low level of population differentiation in POC, comparable to incense-cedar, is consistent with a former widespread distribution. Since it seems unlikely that significant gene flow now occurs between many of the patchy stands in California, the low population divergence may reflect relictual patterns when more gene flow occurred. Low allozyme divergence would indicate fairly recent population fragmentation.

Despite relatively low overall levels of population divergence, the inland and coastal groups had the most regional differentiation. These two areas may have been isolated long enough or subject to distinct enough selection regimes for regional differences in allozyme frequencies to evolve. The inland sites are distinct

ecologically from the coastal sites, and occupy the highest, driest, and coldest environments for the species.

CONSERVATION

The severity of *Phytophthora* disease has focused attention on POC management and conservation. Alternative silvicultural techniques that reduce inoculum and minimize transport of spores are being used (Kliejunas 1985), and strategies to protect POC's genetic diversity are being planned. Although the inland populations of the Scott and Trinity Mountains appear allozymically to be subsets of the coastal populations, the evidence that these stands have been long isolated combined with their unique ecological situation suggests that they be given separate management. Within the inland group, the relatively large genetic differences between the populations sampled indicate that the stands in this region may be more heterogeneous than the stands in the coastal region. Port-Orford-cedar stands in diverse ecological situations in the Scott and Trinity Mountains should be given special attention. Within the coastal group, the Horse Mountain population is important for its relative distinctness from other coastal populations, having both divergent allele frequencies and many unique alleles. The Shelly Creek population is important for its high genetic diversity. In general, the low allozyme distance among other coastal populations and the high proportion of variability within stands indicate that a few large rather than many small protected areas would conserve much of the allozyme diversity in POC.

How adequate is current in situ protection of POC in California? Most POC lands in California that are withdrawn from multiple use are administered by the USDA Forest Service, and some additional areas are administered by the California Department of Parks and Recreation (Table 5). Port-Orford-cedar occurs in only a small proportion of these sites (Table 5). Several areas identified in this study as genetically important are already in protected status, including portions of the Sacramento River population (Cedar Basin Research Natural Area, Castle Crags Wilderness Area, and Castle Crags State Park) and the Horse Mountain population (Horse Mountain Botanical Area). Additional areas should be chosen to increase coverage of these underrepresented areas and to include unrepresented areas such as the northeastern and west-central portions of the coastal distributions and the upper Trinity River drainage.

Ex situ germplasm collections reinforce in situ conservation efforts and extend the range of genetic protection (Ledig 1986, 1988, Millar and Libby 1991). Although there is little direct information on storage of POC seeds, indirect and preliminary evidence suggests that they retain high viability for more than 50 years in cold storage (Allen 1957, Bonner 1990). Seeds should be collected as soon as possible from many stands throughout the range, with special attention to infested areas and dying trees. Such a seed-collection effort would capture genes from dying trees that would otherwise be lost.

Ex situ collections of California POC populations are currently inadequate. Small amounts of seeds remaining from the 180 trees of the current study are kept in cold storage in a seed bank at the Institute of Forest Genetics (USDA Forest Service) in Placerville. Of the public agencies that collect conifer seed for reforestation in California, only the USDA Forest Service has POC seed. Their entire collection in 1988 consisted of 14 pounds of seed from 3 regions, from a total of only 18 trees.

TABLE 5.

Currently established and proposed areas in California where Port-Orford-cedar is protected, with total ha for each area and ha in vegetation types that include Port-Orford-cedar (where available).

Area	Total size (ha)	Types with POC (ha)	References[a]
Wilderness Areas (USDA Forest Service)			
Castle Crags (established)	2,900	<10	T. Keeler-Wolf
Siskiyou (established)	30,470	1,500–6,000[b,c]	K. Wells
Research Natural Areas (USDA Forest Service)			
Adorni (proposed)	244	24	Sawyer 1986
Cedar Basin (proposed)	424	26	Keeler-Wolf 1982
Craigs Creek (proposed)	334	2	T. Jimerson
L.E. Horton (proposed)	528	330[d]	Keeler-Wolf 1986
Rock Creek Butte (proposed)	203	56	Keeler-Wolf 1987b
Upper Goose Creek (proposed)	184	13	Keeler-Wolf 1987a
Botanical Areas (USDA Forest Service)			
Bear Basin (proposed)	396	5–20	K. Wells, T. Jimerson
Horse Mtn. (proposed)	180	12	T. Jimerson
State Parks (California Department of Parks and Recreation)			
Castle Crags (established)	1,740	<5	T. Keeler-Wolf
Wild Rivers (USDA Forest Service)			
Smith River (proposed)	3,908	1,500	K. Wells

[a] Undated references are estimates made from personal communications.
[b] Density and type of POC stands vary greatly.
[c] Estimates for the portion of the Siskiyou Wilderness administered by the Klamath National Forest were not available.
[d] POC occurs in very low densities throughout this type.

The USDA Forest Service has initiated a large program for managing, conserving, and studying POC. Planned within this program are intensive rangewide seed collections, extensive allozyme and common-garden studies that would include over 100 population samples, and a long-term program to screen POC and test its resistance to *Phytophthora*. This program will provide a model approach to genetic management of a threatened forest tree species.

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