

# In Situ Gene Conservation of Six Conifers in Western Washington and Oregon

Sara R. Lipow, Kenneth Vance-Borland, J. Bradley St. Clair, Jan A. Henderson, and Cindy McCain

## ABSTRACT

A gap analysis was conducted to evaluate the extent to which genetic resources are conserved in situ in protected areas for six conifer species in the Pacific Northwest (Sitka spruce, sugar pine, western white pine, ponderosa pine, western redcedar, and western hemlock). The gap analysis involved producing a GIS database detailing the location of protected areas and the distribution and abundance of tree species as inferred from data on potential plant association groups, actual plant associations, and actual land cover type. We used two schemes for stratifying the distribution of each species into genetic populations for gap analysis: seed zones and ecoregions. The results show that most seed zones and ecoregions contain at least 5,000 mature individuals in protected areas, indicating strong in situ gene conservation. Protection is less complete, however, for western white pine in the Puget lowlands, where urbanization and disease have reduced populations below safe levels. These populations represent the highest priority for additional gene conservation. Other species and areas warranting further evaluation include Sitka spruce in some parts of the Puget lowlands, remnant western white pine stands in the Oregon Coast Range, and sugar pine within the white pine blister rust zone.

**Keywords:** Gap analysis, biodiversity, genetic resources, conservation planning, GIS

Forest trees are an integral component of the ecosystems and economy of the Pacific Northwest. Maintenance of well-adapted populations capable of evolving in response to new stresses such as climate change and exotic diseases and to selection for new product traits is therefore of paramount importance to the region. Pacific Northwest conifers typically express higher levels of genetic variation than most other plants (Hamrick et al. 1992), because they experience very diverse conditions during their long lives and across their wide geographic ranges with high levels of gene flow. Responses to selection require genetic variation, but the storehouse of genetic variation in forest trees is potentially threatened by pests and diseases, shifting ecological conditions, urbanization, and conversion of forestlands to agriculture. As continued forest health and productivity require genetic variation, its conservation is recognized as an essential component of responsible forest stewardship (Montréal Process 1999).

Concern over the conservation of genetic variation prompted a group of public and private organizations in western Oregon and Washington to form the Pacific Northwest Forest Tree Gene Conservation Group. The principal mission of this organization was to design and promote cooperative efforts to ensure that the adaptation and evolutionary potential of important tree species is maintained. As part of this effort, we compiled data on genetic resources existing both at their original location (in situ) and at some other location (ex

situ) to identify areas where additional conservation efforts are warranted. Results were reported previously from an analysis of ex situ genetic resources in seed orchards, seed stores, and genetic tests (Lipow et al. 2001). For the eight conifers evaluated, the ex situ collections are extensive and a valuable component of total available genetic resources.

The goal of this in situ analysis is to identify places where large populations of trees are conserved in protected areas, as well as those places where few or no trees are conserved. We extended the techniques of "gap analysis" to apply to genetic variation within species. Gap analysis was originally developed to ascertain whether native animal species and natural communities are represented in present-day conservation lands (Scott and Jennings 1997). It involves creating a GIS to intersect digital maps displaying protected areas with those showing the distribution of biodiversity. Our gap analysis also included data layers representing patterns of genetic variation within species. Here we present results for six species: Sitka spruce [*Picea sitchensis* (Bong.) Carr.], sugar pine (*Pinus lambertiana* Dougl.), western white pine (*Pinus monticola* Dougl. ex D. Don), ponderosa pine (*Pinus ponderosa* Dougl. ex Laws), western redcedar (*Thuja plicata* Donn ex D. Don), and western hemlock [*Tsuga heterophylla* (Raf.) Sarg.]. Results were reported previously for Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*] and noble fir (*Abies procera* Rehd.) (Lipow et al. 2004).

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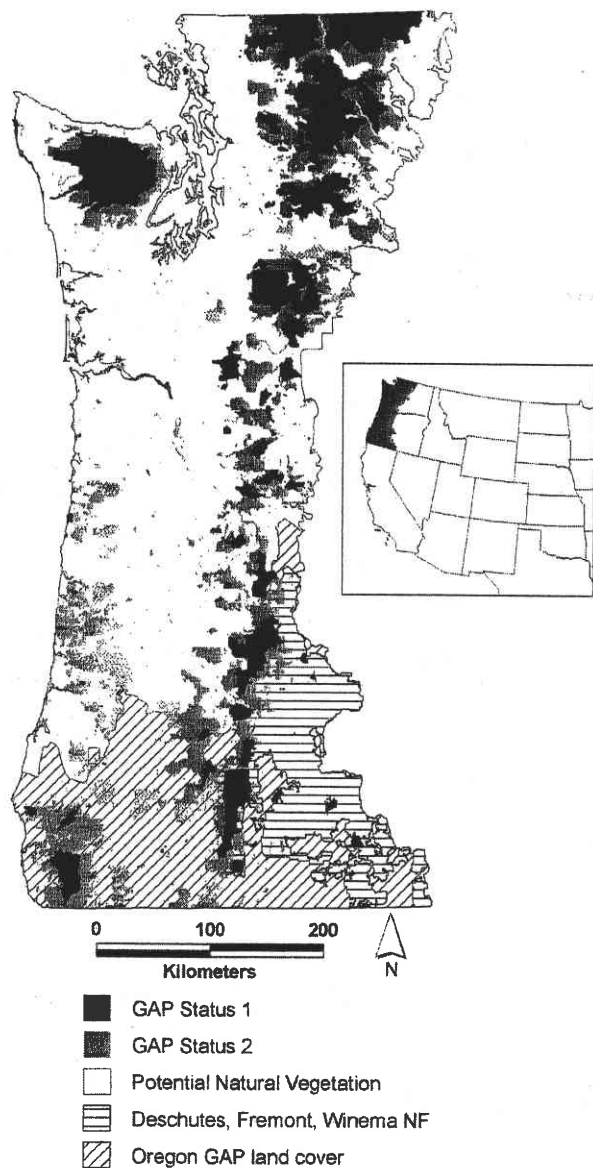


Figure 1. Study area in Oregon and Washington showing the location of status 1 and 2 protected areas and the underlying data layers used to generate tree distribution maps, as modeled by climax plant associations in the potential natural vegetation subregion; climax plant associations mapped with aerial photography in the Deschutes, Fremont, and Winema National Forests (NF); and vegetation mapped with satellite imagery in the Land Cover subregion.

## Methods

A GIS database detailing the location of protected areas, species distributions, and two genetic stratifications was developed for western Oregon and Washington. The eastern boundary was determined by two level III ecoregions, the North Cascades and Eastern Cascades Slope and Foothills (level III ecoregions define provinces or climatic subzones; Pater et al. 1998) (Figure 1), except in southern Washington, where it was set by the availability of species distribution data (see Lipow et al. 2004 for a listing of GIS data layers used).

A protected areas coverage was built following conventions developed by the National GAP Analysis Program (Scott and Jennings

1998). The program assigns land to four status levels. We regarded all status 1 and 2 lands as protected. Management plans for status 1 lands call for maintaining a natural state and allowing natural disturbance events to proceed. Examples include wilderness areas, National Parks, and Nature Conservancy preserves. Status 2 lands are generally managed for natural values, but they may be used in ways that degrade the quality of existing natural communities; examples include National Wildlife Refuges and most state parks. Although status 3 lands have legal mandates that generally prevent permanent land conversion from natural or seminatural habitats to anthropogenic habitats, they are subject to extractive uses, such as timber harvest. Examples include most "matrix" Bureau of Land Management (BLM) and USDA Forest Service lands. We did not consider status 3 lands protected, although they may contain extensive in situ genetic resources. Finally, status 4 lands are managed for extensive human uses. The protected areas coverage (Figure 1) was assembled from available GIS data provided by a variety of sources (Lipow et al. 2004).

The genetic gap analysis required high-resolution distribution maps for each species that detailed the presence and abundance of individuals across the landscape. We derived distribution maps from existing GIS data on potential plant association groups, actual plant associations, and actual land cover types. The quality and type of data varied in different parts of the region (Figure 1). The plant association group (PAG) submodel of the potential natural vegetation (PNV) model (Henderson 1998) served as the basis for the development of tree distribution maps in Washington and northwestern Oregon (Lipow et al. 2004). PAGs are mapping units that represent theoretical climax plant associations. They are defined by the composition of the overstory and understory vegetation (Hall 1998). Plot data, primarily from ecology plots on federal lands but also including a variety of other plots, are used to develop and calibrate the model (Henderson 1997). The study area was stratified into 29 PNV ecozones and contained 75 PAGs. Tree distributions were inferred through a set of tables to predict the density of each species in each PAG by PNV ecozone combination. For each combination, the tables show the expected density of mature individuals of each species, with four density levels modeled: high-density (>100 stems/ha), mid-density (10–100 stems/ha), low-density (1–10 stems/ha), and absent.

PAG grids were not available for the entire study area. For the Deschutes, Fremont, and Winema National Forests, GIS coverages of climax plant associations based on aerial photography and field reconnaissance were obtained; for each forest, a separate table showing the four densities of trees was developed. For the remainder of southern Oregon and other areas in Oregon with no PAG data, we derived tree distributions from the Land Cover coverage produced by the Oregon Gap Analysis Program (Kilgaard 1999). Because the land cover types are generalized and broadly defined, tree distribution grids produced from the coarser Land Cover coverage were expected to have lower accuracy and precision than those produced by the PNV model and the plant association coverages for the three National Forests.

## Accuracy Assessment of Species Distributions

To estimate the accuracy of the resulting species distribution maps, we analyzed data on species occurrences produced by the USDA Forest Service's Pacific Northwest Region Current Vegetation Survey (CVS) (Johnson 1998). The primary sample unit of a CVS plot is a 1-ha area that contains five 0.08-ha, five 0.02-ha, and

**Table 1.** Definitions of protection classes used in the gap analysis, including expected population sizes in protected areas and the entire strata.

| Protection class | Species occurrence | Description of class                            | Minimum expected population size <sup>a</sup> |                          |                                |
|------------------|--------------------|-------------------------------------------------|-----------------------------------------------|--------------------------|--------------------------------|
|                  |                    |                                                 | Entire stratum                                | Status 1 protected areas | Status 1 and 2 protected areas |
| 1                | Common             | Well protected in status 1 areas alone          | >25,000                                       | >5,000                   |                                |
| 1                | Uncommon           | Well protected in status 1 areas alone          | 5,000                                         | >10% of entire stratum   |                                |
|                  |                    |                                                 | 25,000                                        |                          |                                |
| 2                | Common             | Well protected in status 1 and 2 areas combined | >25,000                                       | <5,000                   | >5,000                         |
| 2                | Uncommon           | Well protected in status 1 and 2 areas combined | 5,000                                         | <10% of entire stratum   | >10% of entire stratum         |
|                  |                    |                                                 | 25,000                                        |                          |                                |
| 3                | Common             | Not well protected                              | >25,000                                       |                          | <5,000                         |
| 3                | Uncommon           | Not well protected                              | 5,000                                         |                          | <10% of entire stratum         |
|                  |                    |                                                 | 25,000                                        |                          |                                |

<sup>a</sup> Minimum expected population size calculated as  $\Sigma(\text{ha at high density} \times 100) + \Sigma(\text{ha at mid density} \times 10) + \Sigma(\text{ha at low density})$ .

five 0.004-ha subplots. Species are recorded for all trees >1.219 m dbh in the 1-ha plot, 0.33–1.22 m dbh in the 0.08-ha subplots, 0.08–0.33 m dbh in the 0.02-ha subplots, and 0.03–0.12 m dbh in the 0.004-ha subplots.

In regions where distribution maps were based on the PNV model, the accuracy assessment was restricted to CVS plots in protected areas, where we assumed that actual and potential distributions were equivalent. Because the extent of protected land is limited in the Deschutes, Fremont, and Winema National Forests, however, we examined all CVS plots in those forests regardless of protected status. All CVS plots were also analyzed for areas based on the Land Cover map, because this shows actual vegetation.

The accuracies of the high-, mid-, and absent-density levels were evaluated by comparing pixels on the distribution maps with the data from the corresponding CVS plots. The number of pixels where a species was predicted to occur at either high or mid density was compared with the number of CVS plots in which a species was detected. The low-density level was excluded from these assessments because the CVS plot data are inadequate for determining accuracy. The number of pixels where a species was predicted to be absent was also compared with the number of CVS plots in which a species was not detected.

### Spatial Patterns of Genetic Variation

Two systems were used to stratify each species into populations for analysis: seed zones and ecoregions. Seed zones for Oregon (Randall 1996) and Washington (Randall and Berrang 2002) are designed to inform land managers about the risk associated with moving seed from a source environment to another location during reforestation. Seed zone sizes and boundaries reflect the extent and geographic patterns of genetic variation for each species, as revealed by genecological, isozyme, and seed movement studies. Ponderosa pine, for example, has high local genetic structure, and consequently, its seed zones are small and subdivided into relatively narrow elevational bands. In contrast, western redcedar has less geographic genetic structure, larger seed zones, and wider elevation bands. For our analyses, seed zones were further divided into elevation bands according to the defined elevation intervals (Randall 1996, Randall and Berrang 2002).

Ecoregions were developed by a group of government agencies, including the Environmental Protection Agency and the US Geological Survey, with the intent of providing a spatial framework for environmental resource management (Omernik 1995, Pater et al. 1998). Ecoregions denote areas of general similarity in ecosystems based on environmental factors and vegetation. They do not directly

reflect genetic structure. Nevertheless, because adaptive genetic variation and environmental variation tend to be correlated across a species range, ecoregions can appropriately serve as a stratification, albeit with potentially lower precision, in a genetic gap analysis. Moreover, because ecoregions are widely used by federal and state agencies carrying out conservation assessments, their application here is expected to facilitate integration of these results with those obtained for other taxa. We used the most detailed (level IV) ecoregions for the gap analyses.

### Gap Analyses

The seed zone gap analyses began with a spatial overlay of each seed zone by elevation map with the protected areas map. We then tabulated the area of each density class in each seed zone by elevation by protection stratum for each species. The ecoregion analyses involved combining the ecoregion map with the protected areas map, then tabulating the area of each density class in each ecoregion by protection stratum. Therefore, for each species in each stratum, we had data on the total number of hectares and the number of hectares in status 1 and 2 protection for each density class.

The next step was to assign species in strata to one of three classes of protection, the definitions of which reflect the number of individuals required for conservation of presumably locally adapted populations. Several researchers suggest that an effective population size of 1,000 (Lynch 1996), or a census number of approximately 5,000 (Yanchuk 2001, Yanchuk and Lester 1996), is desirable for gene conservation. For species at high density, 5,000 individuals may be found in a protected area that is only a few hectares large, whereas much larger protected areas are required for populations at lower densities. The definitions of the three classes of protection consider the minimum expected population sizes of species in strata as a whole and in status 1 and 2 protected areas (Table 1). Minimum expected population sizes are approximated as  $\Sigma(\text{ha at high density} \times 100) + \Sigma(\text{ha at mid density} \times 10) + \Sigma(\text{ha at low density})$ .

Protection class 1 is defined as well protected in status 1 protected areas, class 2 is defined as well protected considering both status 1 and 2 protected areas, and class 3 is defined as not well protected in either status 1 or 2 protected areas. Strata in which species are extremely rare (minimum expected population size <5,000) were not classified.

## Results

### Species Distribution Maps and Accuracy Assessment

We derived high-resolution maps showing the distribution and abundance of each of six conifer tree species (panel A in Figures

**Table 2.** The number of current vegetation survey plots for which each species was predicted to be present or absent and, of these, the number of plots validated.

| Map prediction     | PNV <sup>a</sup> model subregion |                  |       | Deschutes, Fremont, and Winema NFs |                  |       | Land cover subregion |                  |       |
|--------------------|----------------------------------|------------------|-------|------------------------------------|------------------|-------|----------------------|------------------|-------|
|                    | Number predicted                 | Number validated | Ratio | Number predicted                   | Number validated | Ratio | Number predicted     | Number validated | Ratio |
| Sitka spruce       |                                  |                  |       |                                    |                  |       |                      |                  |       |
| Present            | 71                               | 43               | 0.606 |                                    |                  |       |                      |                  |       |
| Absent             | 613                              | 593              | 0.967 |                                    |                  |       | 1381                 | 1381             | 1.000 |
| Sugar pine         |                                  |                  |       |                                    |                  |       |                      |                  |       |
| Present            |                                  |                  |       | 20                                 | 10               | 0.500 | 557                  | 208              | 0.373 |
| Absent             |                                  |                  |       | 1170                               | 1113             | 0.951 | 116                  | 102              | 0.879 |
| Western white pine |                                  |                  |       |                                    |                  |       |                      |                  |       |
| Present            | 64                               | 46               | 0.719 | 88                                 | 72               | 0.818 | 27                   | 23               | 0.852 |
| Absent             | 752                              | 685              | 0.911 | 1160                               | 1132             | 0.976 | 326                  | 307              | 0.942 |
| Ponderosa pine     |                                  |                  |       |                                    |                  |       |                      |                  |       |
| Present            | 101                              | 74               | 0.733 | 1111                               | 1084             | 0.976 | 590                  | 160              | 0.271 |
| Absent             | 1329                             | 1257             | 0.946 | 139                                | 80               | 0.576 | 528                  | 470              | 0.890 |
| Western redcedar   |                                  |                  |       |                                    |                  |       |                      |                  |       |
| Present            | 1011                             | 530              | 0.524 |                                    |                  |       | 230                  | 59               | 0.257 |
| Absent             | 778                              | 740              | 0.951 |                                    |                  |       | 1158                 | 1130             | 0.976 |
| Western hemlock    |                                  |                  |       |                                    |                  |       |                      |                  |       |
| Present            | 1820                             | 1276             | 0.701 |                                    |                  |       | 230                  | 91               | 0.396 |
| Absent             | 669                              | 621              | 0.928 |                                    |                  |       | 315                  | 312              | 0.990 |
| Average            |                                  |                  |       |                                    |                  |       |                      |                  |       |
| Present            |                                  |                  | 0.657 |                                    |                  | 0.765 |                      |                  | 0.430 |
| Absent             |                                  |                  | 0.941 |                                    |                  | 0.834 |                      |                  | 0.946 |

<sup>a</sup> PNV, potential natural vegetation; NF, National Forest.

2–7). As expected, maps were most accurate in Washington and northwestern Oregon where they were based on plant association groups as predicted by the PNV model, and in the Deschutes, Fremont, and Winema National Forests where they were based on plant associations mapped using aerial photography and field reconnaissance (Table 2). They were less satisfactory for the area in southern Oregon where they were extrapolated from more coarsely mapped land cover types. Conclusions from the gap analysis are therefore tentative for the latter area.

The accuracy assessment shows that species were detected on an average of 65.7 percent (range, 52.4–73.3 percent) of the plots for which the PAG distribution maps predicted presence at mid or high density (Table 2). Conversely, species were not detected on an average of 94.1 percent (range, 91.1–96.7 percent) of the plots where the maps predicted absence. The western hemlock, ponderosa pine, and western white pine maps appeared to be better representations of true distributions than the ones for western redcedar and Sitka spruce. Validation percentages from the accuracy assessment were also high for the Deschutes, Winema, and Fremont National Forests, averaging 76.5 percent (range, 50.0–97.6 percent) for species presence and 83.4 percent (range, 57.6–97.6 percent) for species absence. The lowest value for these Forests was for sugar pine presence (50.0 percent). For the Land Cover subregion, the predictions of the tree distribution maps were less robust. Although species seldom occupied areas where their absence was predicted (accuracy average, 94.6 percent; range, 87.9–100 percent), they sometimes did not occur at locations where their presence was predicted (accuracy average, 43.0 percent; range, 25.7–85.2 percent). Indeed, for species presence, only western white pine had an accuracy exceeding 50 percent for the Land Cover subregion.

### Gap Analysis

The gap analysis results predicted that for most regional seed zones and ecoregions, genetic resources of the six conifers examined are well protected in status 1 and 2 protected areas (Figures

2–7). Nineteen of the 185 (10.3 percent) species by seed zones strata and 39 of the 215 (18.1 percent) species by ecoregions ranked in class 3 indicating possible gaps (Table 3). Closer examination revealed that many of the conservation gaps in class 3 strata are likely not biologically significant. First, some strata have few trees, yet in adjacent strata the species was common, presumably genetically similar, and well protected. Such strata usually occurred at the margin of a species range or at the highest or lowest elevation bands within a seed zone. Second, for some strata, local resource experts or other data confirmed that the number of protected trees exceeded 5,000 despite the lower minimum estimate from the distribution map. Third, some strata contained little area in status 1 and 2 protected lands, but most of these acres are managed in a manner consistent with maintenance of genetic variation. For example, few acres on the Fremont and Winema National Forest met the strict criteria of status 1 or 2 protection, but in these Forests, many trees are excluded from timber harvesting by various management requirements. Fourth, some class 3 ecoregions are inappropriately small representations of unique populations given the extent and structure of species genetic variation.

### Sitka Spruce

The results of both the seed zone and ecoregion analyses showed that Sitka spruce genetic resources are extensively conserved along the coast, with some less well conserved areas further inland (Table 3; Figure 2). In Washington, apparent genetic resource gaps were found for much of the Puget lowlands. Five class 3 ecoregions (2a, 2b, 2c, 2d, and 2f) surrounding the Puget lowlands correspond to a single seed zone (WA3) categorized as class 2 (well protected in status 2 protected areas). Ecoregion 2a (Fraser lowlands) contains few protected areas and appeared as a gap for all species present in that area. In 2b (eastern Puget riverine lowlands), Sitka spruce is a major component of the natural vegetation, yet most protected areas are largely tidal and intertidal marshes inappropriate for this species.

**Table 3. Results from the gap analysis showing minimum expected population sizes in the stratum as a whole and in protected areas for all seed zones and ecoregions in protection class 3.**

| Seed zone or ecoregion in protection class 3        | Minimum expected population size |                             |                                   |
|-----------------------------------------------------|----------------------------------|-----------------------------|-----------------------------------|
|                                                     | Stratum                          | Status 1<br>protected areas | Status 1 and 2<br>protected areas |
| <b>Sitka spruce</b>                                 |                                  |                             |                                   |
| WA4: Puget Sound                                    | 68,362                           | 39                          | 465                               |
| WA5: Lower Columbia River                           | 16,074                           | 0                           | 47                                |
| 1h: Southern Oregon coastal mountains               | 126,004                          | 163                         | 1,182                             |
| 2a: Fraser lowlands                                 | 149,846                          | 0                           | 885                               |
| 2b: Eastern Puget riverine lowlands                 | 106,962                          | 0                           | 455                               |
| 2c: San Juan Islands                                | 5,434                            | 3                           | 12                                |
| 2d: Olympic rainshadow                              | 308,510                          | 377                         | 2,860                             |
| 2f: Central Puget lowlands                          | 282,973                          | 235                         | 1,030                             |
| 4a: Western Cascade Lowlands and Valleys            | 8,503                            | 0                           | 0                                 |
| 78f: Coastal Siskiyou                               | 46,760                           | 220                         | 2,372                             |
| <b>Sugar pine</b>                                   |                                  |                             |                                   |
| 9b: Grand fir mixed forest                          | 6,234                            | 152                         | 463                               |
| 9g: Klamath/Goose Lake warm wet basins              | 41,328                           | 0                           | 3,531                             |
| 9h: Fremont pine/fir forest                         | 155,896                          | 490                         | 602                               |
| 9j: Klamath juniper/ponderosa pine woodland         | 20,187                           | 223                         | 227                               |
| <b>Western white pine</b>                           |                                  |                             |                                   |
| OR6: Oregon Coast Range <sup>1</sup>                | 2,238                            | 0                           | 0                                 |
| OR17: Klamath                                       | 164,946                          | 3,410                       | 3,410                             |
| OR18: Lakeview                                      | 62,559                           | 0                           | 0                                 |
| 1e: Outwash                                         | 24,108                           | 0                           | 731                               |
| 1f: Willapa hills                                   | 241,573                          | 699                         | 970                               |
| 2a: Fraser lowland                                  | 81,749                           | 0                           | 439                               |
| 2b: Eastern Puget riverine lowlands                 | 156,831                          | 0                           | 1,249                             |
| 2e: Eastern Puget uplands                           | 221,322                          | 207                         | 1,773                             |
| 2f: Central Puget lowlands                          | 375,084                          | 330                         | 2,828                             |
| 2g: Southern Puget prairies                         | 196,111                          | 280                         | 1,247                             |
| 2h: Cowlitz/Chehalis foothills                      | 88,921                           | 0                           | 45                                |
| 2i: Cowlitz/Newaukum prairie floodplains            | 86,274                           | 0                           | 293                               |
| 78a: Rogue/Illinois valleys                         | 7,811                            | 58                          | 974                               |
| 78c: Umpqua interior foothills                      | 41,107                           | 0                           | 966                               |
| 9h: Fremont pine/fir forest                         | 83,296                           | 0                           | 0                                 |
| <b>Ponderosa pine</b>                               |                                  |                             |                                   |
| OR1 (0–305 m) Hood River                            | 118,635                          | 335                         | 3,060                             |
| OR3 (1830–2134 m) Crater Lake                       | 66,647                           | 178                         | 2,009                             |
| OR7 (>2135 m) Lakeview                              | 49,098                           | 0                           | 0                                 |
| OR7 (1220–1524 m) Lakeview                          | 29,876                           | 0                           | 0                                 |
| OR7 (1525–1829 m) Lakeview                          | 949,525                          | 0                           | 0                                 |
| OR7 (1830–2134 m) Lakeview                          | 1,475,009                        | 0                           | 0                                 |
| OR8 (1830–2134 m) Klamath                           | 59,147                           | 0                           | 0                                 |
| OR11 Willamette Valley                              | 443,128                          | 407                         | 528                               |
| OR12 (0–305 m) Umpqua                               | 41,574                           | 146                         | 421                               |
| OR14 (306–610 m) Eagle Point                        | 182,032                          | 421                         | 2,444                             |
| OR15 (306–610 m) South Interior                     | 60,097                           | 196                         | 3,534                             |
| WA1: Puget lowlands <sup>2</sup>                    |                                  |                             |                                   |
| 3b: Willamette River and tributaries gallery forest | 209,967                          | 31                          | 214                               |
| 3c: Prairie terraces                                | 147,879                          | 1,425                       | 3,311                             |
| <b>Western redcedar</b>                             |                                  |                             |                                   |
| 2a: Fraser lowlands                                 | 822,960                          | 0                           | 4,400                             |
| 2h: Cowlitz/Chehalis foothills                      | 909,785                          | 0                           | 454                               |
| 2i: Cowlitz/Newaukum prairie floodplains            | 868,565                          | 0                           | 2,974                             |
| 78e: Inland Siskiyou                                | 34,085                           | 0                           | 24                                |
| 9d: Ponderosa pine/bitterbrush woodland             | 31,862                           | 1                           | 1,618                             |
| <b>Western hemlock</b>                              |                                  |                             |                                   |
| OR5 (915–1219 m) Willamette Valley                  | 29,013                           | 0                           | 0                                 |
| OR6 (0–305 m) Southern Valley                       | 176,710                          | 1,983                       | 3,517                             |
| 2a: Fraser lowlands                                 | 874,136                          | 0                           | 4,487                             |
| 2h: Cowlitz/Chehalis foothills                      | 1,549,026                        | 0                           | 818                               |
| 2i: Cowlitz/Newaukum prairie floodplains            | 1,060,387                        | 0                           | 4,293                             |
| 3a: Portland/Vancouver basin                        | 13,866                           | 58                          | 1,258                             |
| 3b: Willamette River and tributaries gallery forest | 214,194                          | 0                           | 0                                 |
| 3c: Prairie terraces                                | 382,747                          | 646                         | 2,908                             |
| 78a: Rogue/Illinois Valleys                         | 5,139                            | 7                           | 85                                |
| 78b: Siskiyou foothills                             | 51,618                           | 329                         | 3,385                             |

<sup>1</sup> For western white pine, the Coast Range seed zone was ranked in class 3 even though its minimum estimated populations size was <5,000 because historic records confirmed species occurrences in the zone.

<sup>2</sup> The Puget Lowlands contain only one known ponderosa pine population. It is well protected and was not included in the modeled species distribution (see Results).

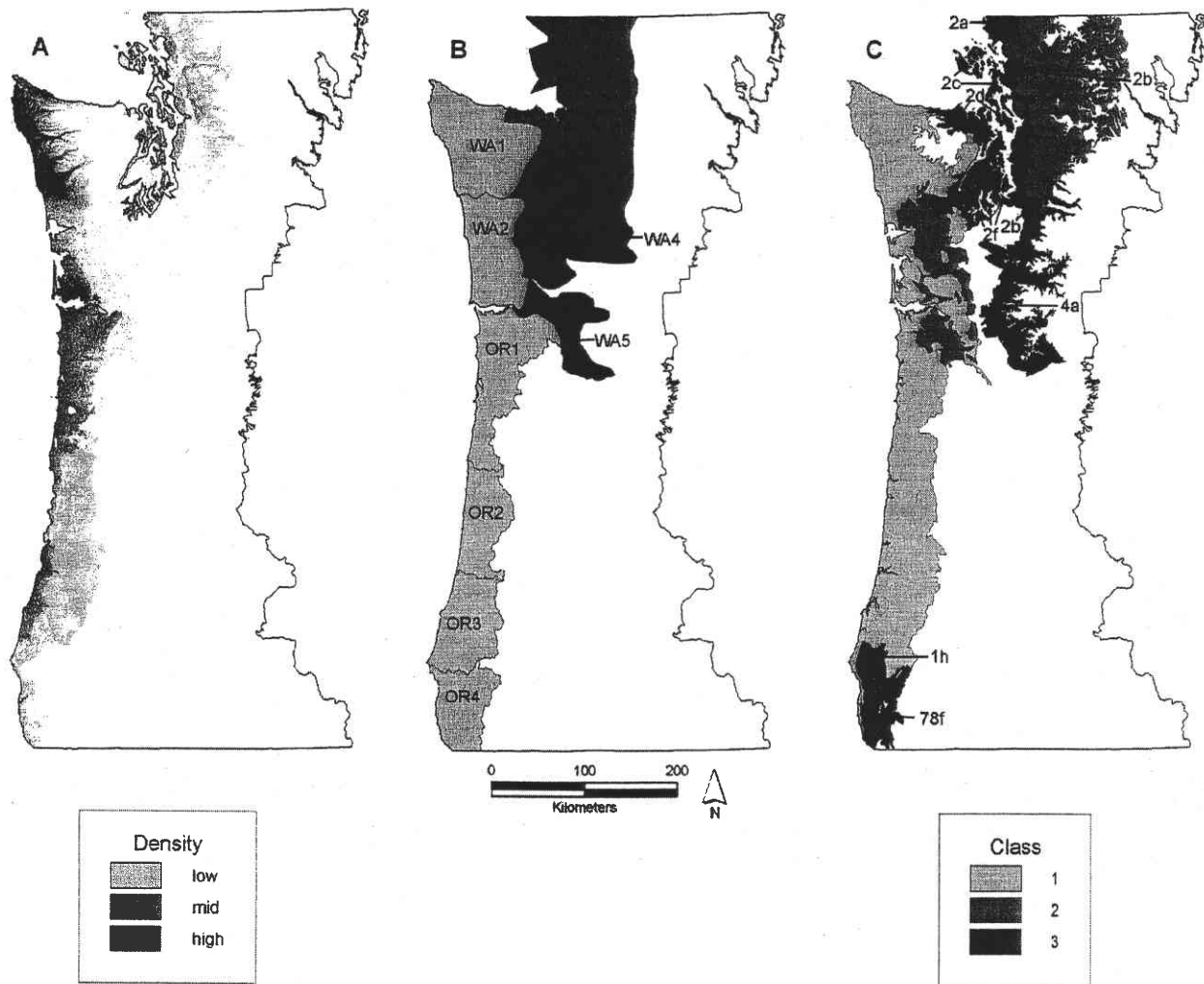


Figure 2. Sitka spruce species distribution and density (A), seed zones categorized according to the gap analysis results (B), and ecoregions categorized according to the gap analysis results with class 3 ecoregions labeled (C).

At least one Sitka spruce population in 2c (San Juan Islands) is protected in Moran State Park. Sitka spruce is also found in several state parks in 2d (Olympic rainshadow), and the actual number of mature trees in protected areas may exceed the minimum expected population size estimate of 2,860. Protection is more limited in the urbanized ecoregion 2f (central Puget lowlands).

We also found a possible gap south of Puget Sound in seed zone WA4, but Sitka spruce can be found in several protected areas scattered across the zone. Again, the minimum expected population size may underestimate the actual number of protected trees. Another seed zone that was in protection class 3 was WA5 along the Columbia River; however, many trees can be found protected in a Nature Conservancy preserve in the southwestern corner of the zone and two wildlife refuges that lie just a few kilometers west of the zone boundary.

The analysis for Sitka spruce in Oregon showed that the species is well protected everywhere, apart from ecoregions 1h (southern Oregon coastal mountains) and 78f (coastal Siskiyou). Several nearby populations closer to the coast in ecoregions 1a and 1b are well protected.

### Sugar Pine

Although the seed zone gap analysis suggests that protected populations of sugar pine occur throughout the species range in Oregon, the ecoregion analysis detected four class 3 strata (Table 3; Figure 3). The species distribution extends only slightly into ecoregion 9b (grand fir mixed forest), and the species is well protected in adjoining strata. Ecoregions 9g (Klamath/Goose Lake warm wet basins), 9h (Fremont pine/fir forest), and 9j (Klamath juniper/ponderosa pine woodland) are adjacent to each other. Although there is little status 1 and 2 protected land in these areas, stands of sugar pine on status 3 National Forest lands are extensive.

### Western White Pine

We found that genetic resources are sufficiently conserved for many western white pine strata, although some apparent gaps were uncovered in some ecoregions and seed zones (Table 3; Figure 4). In Washington, the ecoregion analysis indicates that possible gaps exist in seven Puget lowlands ecoregions (2a, 2b, 2e, 2f, 2g, 2h, and 2i) and two adjacent Washington Coast Range ecoregions (1e and 1f). Some trees can be found in Moran State Park in Kitsap County

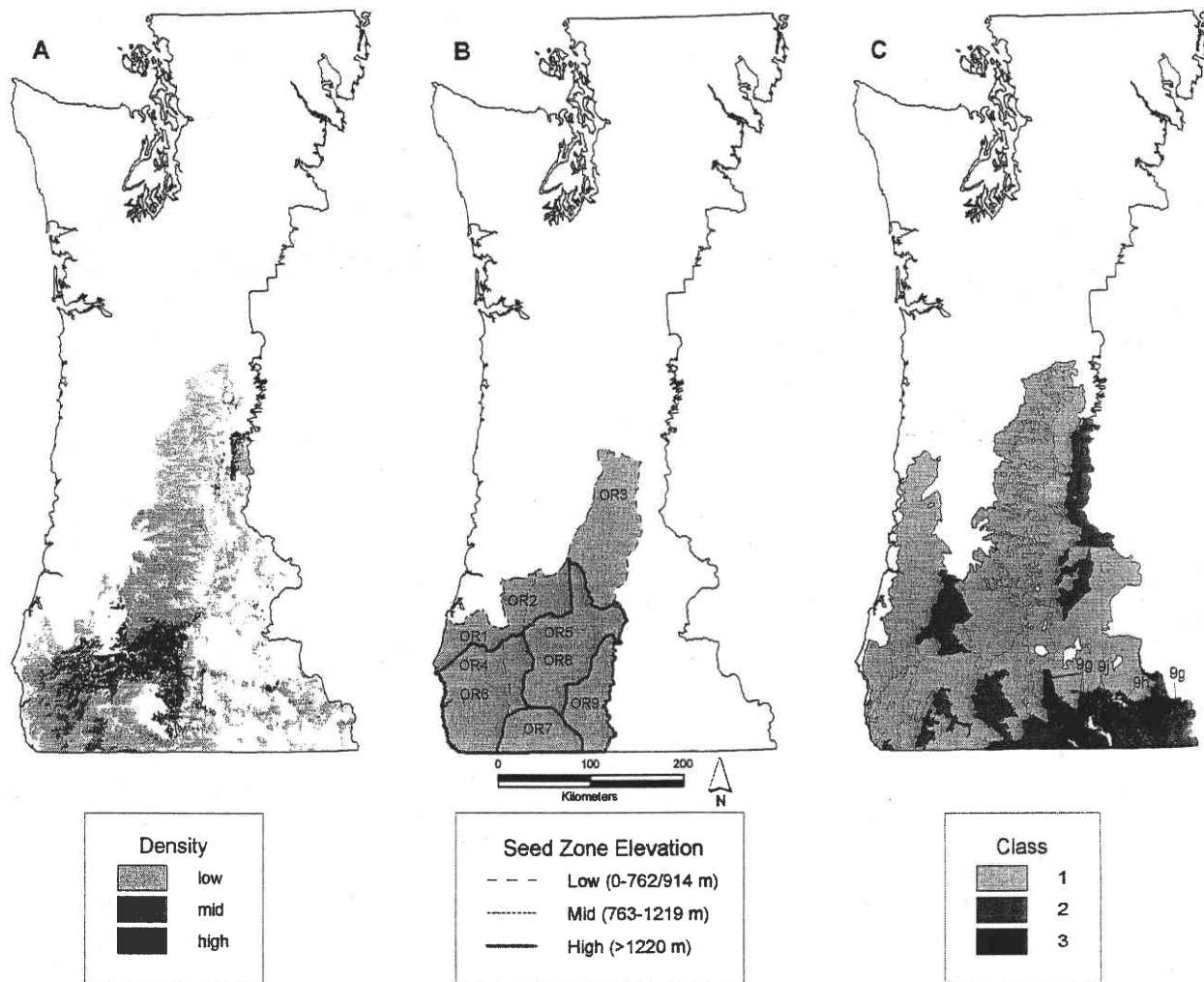


Figure 3. Sugar pine species distribution and density (A), seed zones categorized according to the gap analysis results (B), and ecoregions categorized according to the gap analysis results with class 3 ecoregions labeled (C).

(ecoregion 2c) and in Shoreline Park in northwestern King County (ecoregion 2f). We have not identified any ex situ collections of western white pine germ plasm from the Puget lowlands (Lipow et al. 2001).

In Oregon, gaps apparently exist in three seed zones and three ecoregions. Seed zone OR6 represents an area in the Oregon Coast Range where western white pine once occurred more frequently, although it was probably never common (Critchfield and Little 1966). Today, a few scattered stands remain on state- and industry-owned lands (Alan Kanaskie, Oregon Department of Forestry, personal communication, 2005). The OR6 seed zone overlaps with ecoregion 1g, which is considered class 2 because it contains areas where western white pine is more abundant. Western white pine is infrequent throughout the large class 3 seed zone OR17 in south central Oregon, but the number of individuals protected in Gearhart Mountain Wilderness Area may exceed the minimum expected population size estimate of 3,410. Seed zone OR18 has little protected area and is categorized as a gap for both western white pine and ponderosa pine.

There are two other putative gaps for western white pine in southern Oregon. Western white pine is quite rare in ecoregion 78a

(Rogue/Illinois Valley), although more than 5,000 individuals are found in the Illinois Valley Botanical Emphasis Area and Rough and Ready Flat, two protected areas that extend from ecoregion 78a into ecoregion 78d (class 1). Western white pine is somewhat more abundant in the Umpqua interior foothills (ecoregion 78c), but protected areas in the ecoregion are limited. The genetic resources of western white pine are well protected in all nearby ecoregions.

### Ponderosa Pine

Genetic resources for ponderosa pine are adequately conserved throughout the strata in Washington, despite the class 3 categorization of seed zone WA1 (Table 3; Figure 5). This zone encircles the only native population of ponderosa pine in the Puget Sound area, which is located in a 1,000-ha woodland on Fort Lewis. The Army and The Nature Conservancy have established a partnership to protect this unique resource and have designated the area as a Research Natural Area.

In Oregon, we found 11 seed zones and 2 ecoregions with apparent gaps. A gap appears in the Willamette Valley in seed zone OR11 and corresponding ecoregions 3b (Willamette River and tributaries gallery forest) and 3c (Willamette prairie terraces). In the Hood

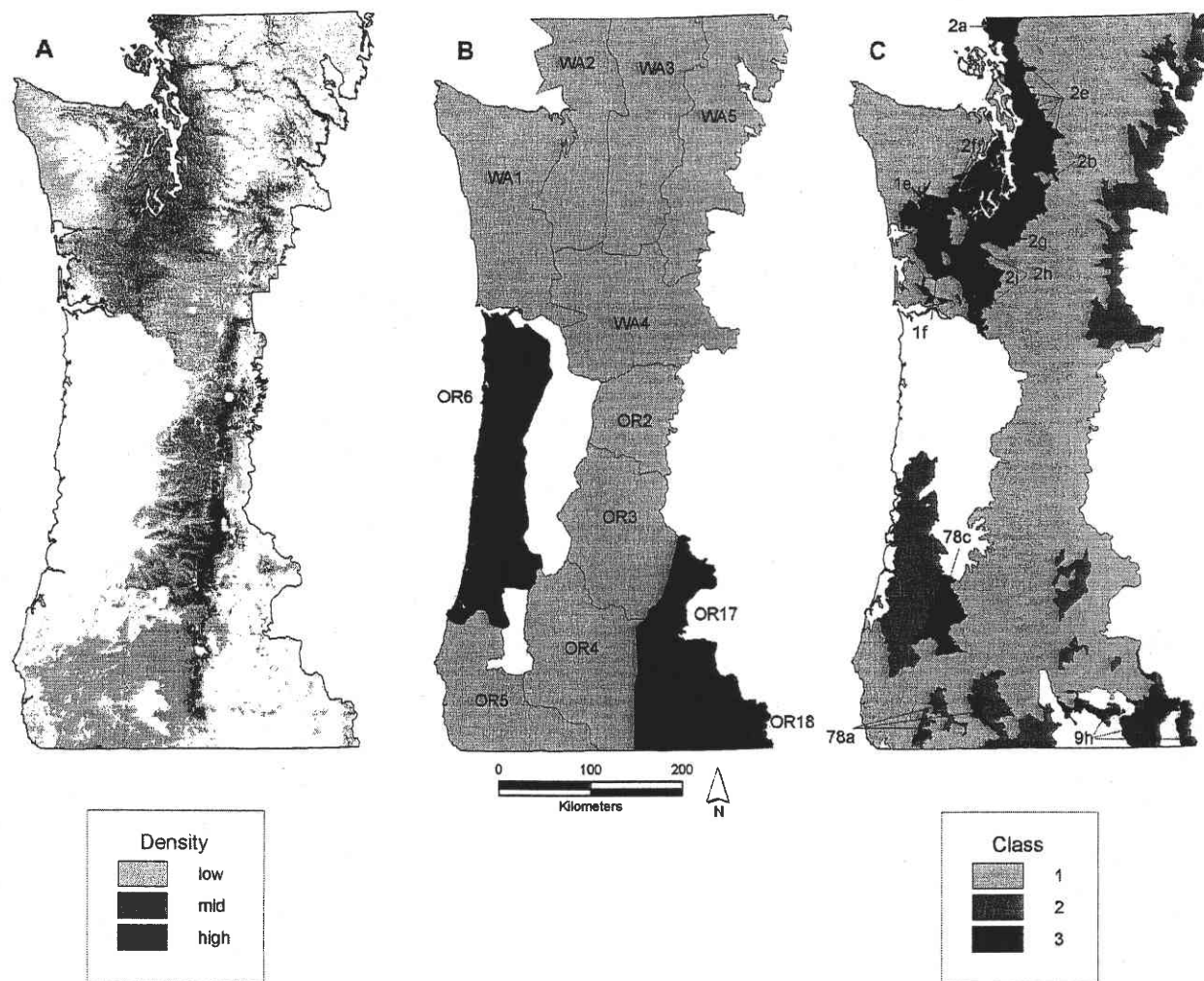


Figure 4. Western white pine species distribution and density (A), seed zones categorized according to the gap analysis results (B), and ecoregions categorized according to the gap analysis results with class 3 ecoregions labeled (C).

River seed zone (OR1), the class 3 elevation band 0–305 m is restricted to a small area along the Columbia River. The minimum expected population size in two state parks in this stratum was 3,060, although ponderosa pine was well protected in the next highest elevation band. Another class 3 stratum occurs in the Crater Lake seed zone: OR3 (1,830–2,134 m). Crater Lake National Park contains some acreage at this elevation, but most of the ponderosa pine occupies status 3 sites in the zone's eastern quarter. Selections from this stratum exist in ex situ reserves (Lipow et al. 2001). OR7 is a small seed zone located in south central Oregon; all four elevation bands were categorized as class 3. In this zone, extensive pine woodlands remain throughout the Lakeview District of the Fremont National Forest, where most logged stands were regenerated via natural regeneration or planting with local seed.

Another apparent gap for ponderosa pine occurred at the highest peaks in the Klamath seed zone OR8 (1,830–2,134 m). This stratum contains no status 1 or 2 protected areas, but the adjacent elevation band in OR8 ranked in class 1. Ponderosa pine genetic resources were not well protected at the lowest elevations (<305 m) of the Umpqua seed zone (OR12), but the next higher elevation band was categorized as class 2. In a low elevation band (306–610 m) of the Eagle Point seed zone (OR14), the minimum expected population size in protected areas

was estimated to be 2,500. Thousands of additional trees were found on status 3 lands managed by the BLM and Rogue River National Forest, and genetic resources were well protected in the same elevation band in neighboring seed zone OR13. The lowest elevation band (306–610 m) in the South Interior seed zone (OR15) was also categorized as class 3; in adjoining seed zones, the same elevation band was categorized as class 1 in OR13 and class 3 in OR14.

#### Western Redcedar

No gaps were found based on the seed zone analysis for western redcedar, but the ecoregional analyses indicated five possible gaps (Table 3; Figure 6). Three of these were in the Puget lowlands (2a, 2h, and 2i); these ecoregions have few protected areas and emerged as possible gaps for several species. The two remaining class 3 ecoregions were in Oregon. The range of western redcedar includes only the eastern edge of the ponderosa pine/bitterbrush woodland ecoregion (9d). The species was very well protected immediately to the west in ecoregion 4c (Cascade Crest montane forest). The class 3 categorization of the inland Siskiyou ecoregion (78e) was probably incorrect because the distribution map in ecoregion 78e is based on

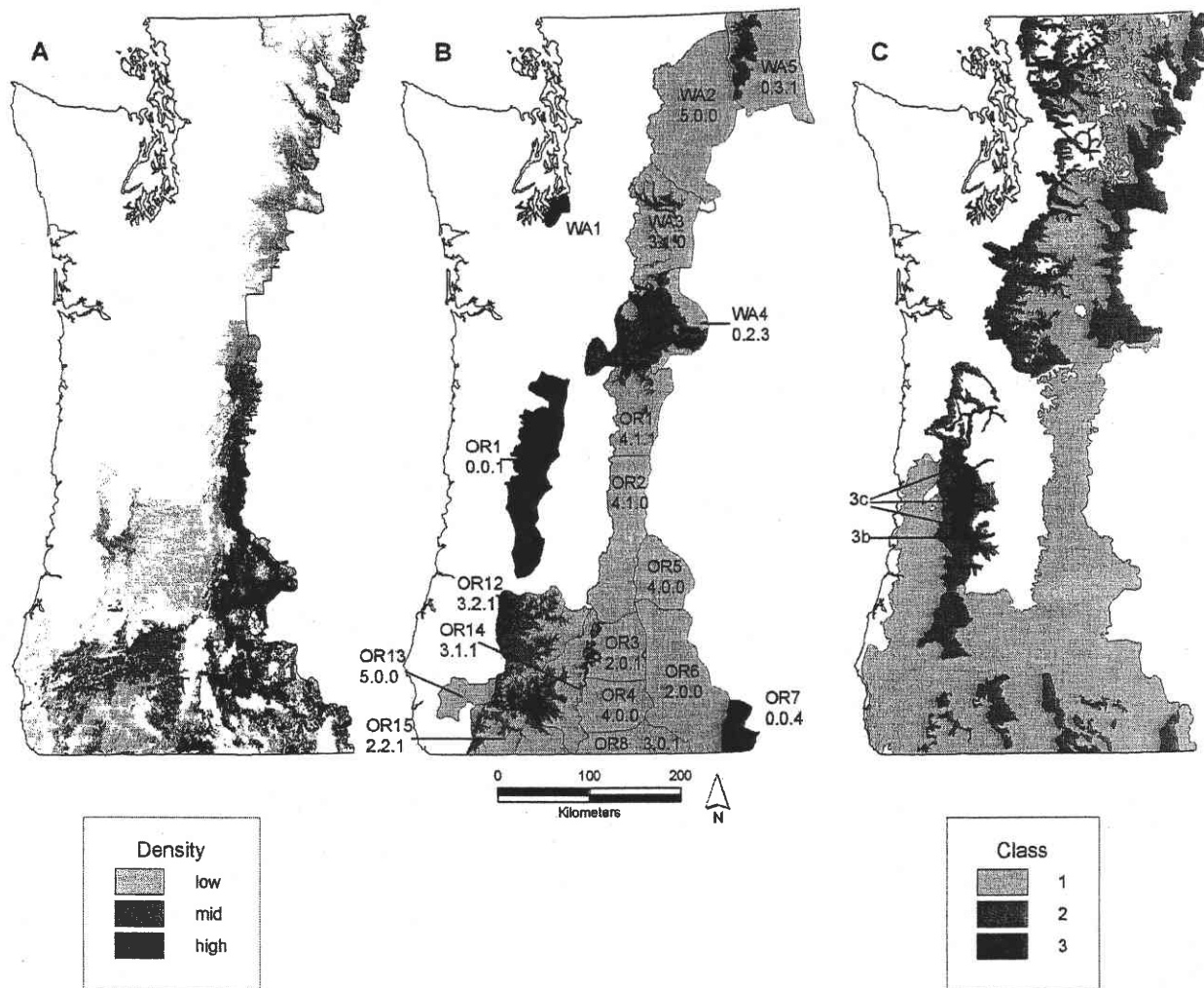


Figure 5. Ponderosa pine species distribution and density (A), seed zones categorized according to the gap analysis results (B), and ecoregions categorized according to the gap analysis results with class 3 ecoregions labeled (C). Each seed zone is labeled and assigned a three-digit code, where the first value indicates the number of elevation bands assigned to class 1, the second indicates the number assigned to class 2, and the third indicates the number assigned to class 3. Within seed zones, each elevation band is shaded according to its gap analysis categorization. In some cases, class 2 and 3 elevation bands include only a small fraction of the total area. Seed zone WA6 was not analyzed since it mostly falls outside of the study area, and only two of four elevation bands in OR6 were examined.

the Land Cover coverage, and it underestimated the extent of western redcedar in the northern section of the ecoregion.

### Western Hemlock

The analysis for western hemlock in Washington indicated that gene conservation is sufficient in all but three ecoregions (2a, 2h, and 2i) (Table 3; Figure 7). As mentioned previously, these ecoregions have few protected areas and contained gaps for several species. The minimum expected population size of western hemlock was estimated to be 4,400 in 2a and 5,111 in 2h plus 2i. Western hemlock genetic resources appeared to be well protected (class 1) in all adjacent ecoregions to the east and west and in the corresponding seed zone.

Although western hemlock was effectively protected in most seed zones and ecoregions in Oregon, there were some exceptions. Four class 3 strata were found in the Willamette Valley, where the natural distribution of western hemlock is limited and protected areas tend to be small. The highest elevation band

(915–1,219 m) for the Willamette Valley seed zone (OR 5) was class 3, contained little total area, and bordered OR3 where the same elevation band was categorized as class 2. Western hemlock was relatively rare in class 3 ecoregions 3a and 3c, but some trees did occur in protected areas. The distribution of western hemlock in ecoregion 3b was restricted to the southernmost quarter of the ecoregion, and the species was well protected in all adjacent ecoregions. Additional class 3 strata were located in the interior valleys of southern Oregon. The lowest strata (0–305 m) in seed zone OR6 was categorized as class 3, included little total land, and extended inland from valleys in OR4, where the same elevation band was categorized as class 1. OR4 and OR6 overlapped with class 3 ecoregions 78a and 78b. Two sizable protected areas were found in ecoregions 78a and 78b, yet most western hemlock occupies higher elevation sites with few protected areas. Western hemlock was well protected in all ecoregions surrounding 78a and 78b.

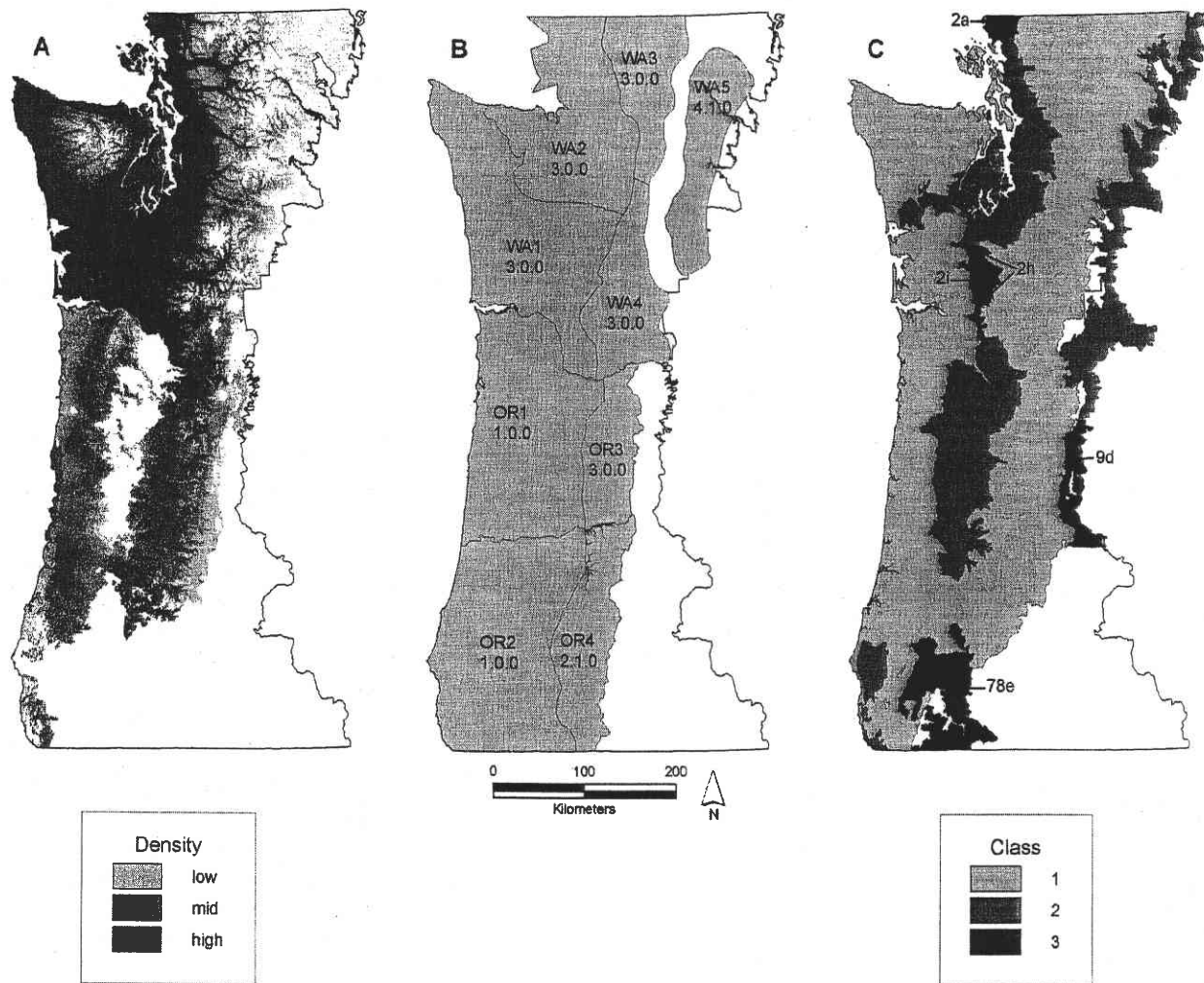


Figure 6. Western redcedar species distribution and density (A), seed zones categorized according to the gap analysis results (B), and ecoregions categorized according to the gap analysis results with class 3 ecoregions labeled. (C) Each seed zone is labeled and assigned a three-digit code, where the first value indicates the number of elevation bands assigned to class 1, the second indicates the number assigned to class 2, and the third indicates the number assigned to class 3. Within seed zones, each elevation band is shaded according to its gap analysis categorization. In some cases, class 2 and 3 elevation bands include only a small fraction of the total area.

## Discussion

Our gap analyses revealed that much of the genetic resources of six important conifers are protected in situ. Although some exceptions exist, most seed zones and ecoregions contain at least 5,000 mature individuals of each species on sites unlikely to be harvested during the next several decades. In most cases, the number of protected trees is much greater. In addition, the majority of strata include populations in status 1 protected areas. Therefore, in the unlikely event of future unsustainable logging in Late Successional Reserves or other status 2 protected areas, genetic resources would remain safe.

For Sitka spruce, conservation of genetic resources is most complete in Oregon, on the west side of the Olympic Peninsula in Washington, and in southwestern Washington near the coast. Fewer trees occur in status 1 and 2 protected areas in the lowlands surrounding Puget Sound. Populations are in decline in the southern Puget lowlands although some protected populations are there as well. If genetic structure is appropriately represented by seed zones, rather than ecoregions, then the remaining protected individuals should be adequate for gene con-

servation. Given the extent of population reduction, however, additional research into the genetic structure of Sitka spruce would be desirable for the entire Puget Lowlands.

The gap analysis results for sugar pine indicated that protected populations occur in all seed zones and most ecoregions. The exceptions are ecoregions in areas with extensive forests classified as status 3 on federal lands. Results in those areas, however, must be interpreted cautiously. The analysis relied heavily on lower resolution data from the Oregon Land Cover coverage and did not consider disease. Sugar and western white pine populations are being decimated by white pine blister rust, especially in the western parts of the species' ranges. Therefore, in strata rife with blister rust, the gap analysis assumption that the potential (i.e., theoretical climax) abundance and distribution of species is predictive of the actual abundance and distribution in protected areas is likely to be violated. Instead, the number of individuals transmitting their genes to the next generation is probably smaller than estimated.

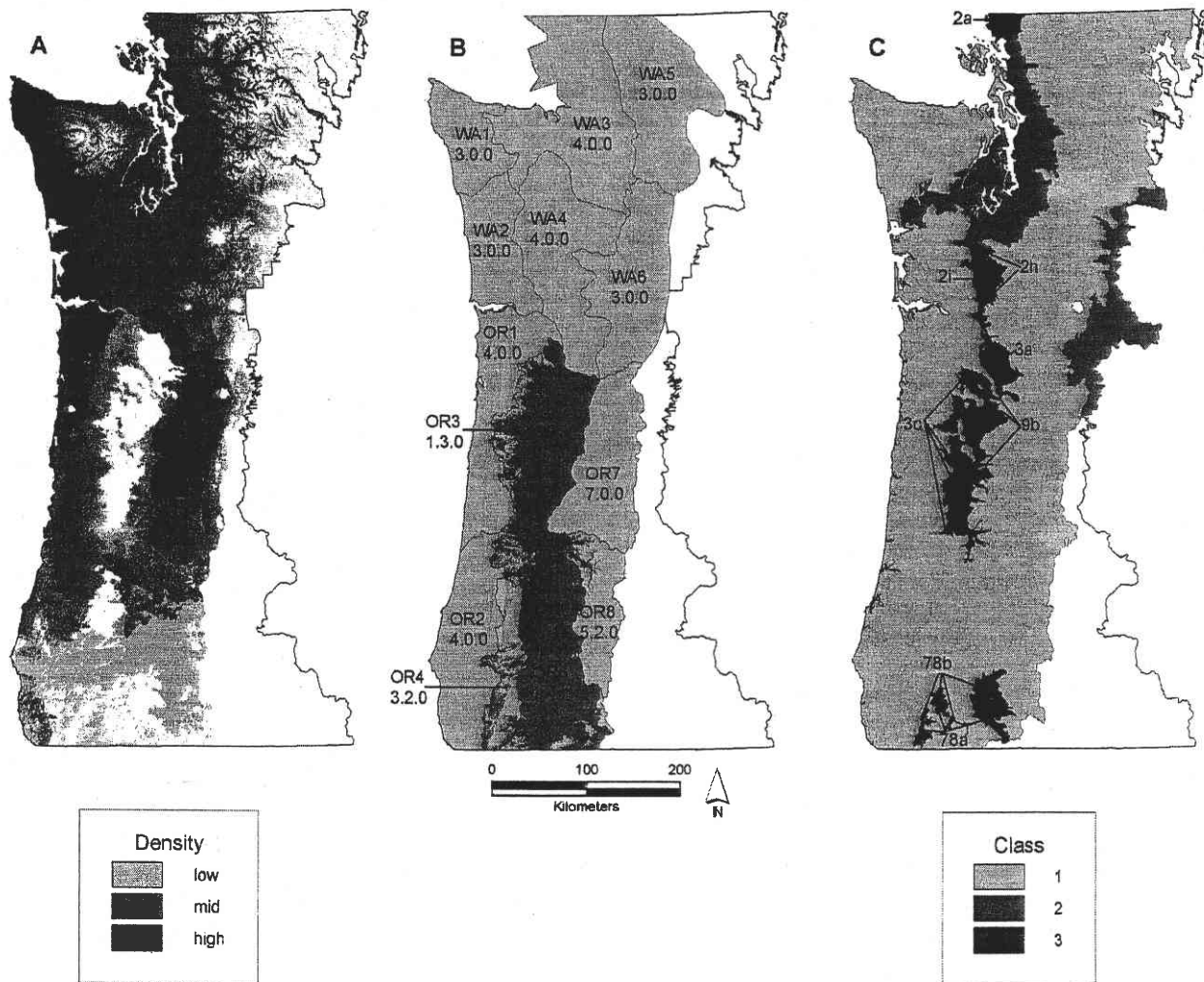


Figure 7. Western hemlock species distribution and density (A), seed zones categorized according to the gap analysis results (B), and ecoregions categorized according to the gap analysis results with class 3 ecoregions labeled. (C) Each seed zone is labeled and assigned a three-digit code, where the first value indicates the number of elevation bands assigned to class 1, the second indicates the number assigned to class 2, and the third indicates the number assigned to class 3. Within seed zones, each elevation band is shaded according to its gap analysis categorization. In some cases, class 2 and 3 elevation bands include only a small fraction of the total area.

Even though blister rust was not accounted for, the gap analysis for western white pine is helpful for directing conservation priorities. The ecoregion analysis suggests that few western white pine populations remain intact in the Puget lowlands. In addition, blister rust, which was first introduced into the western United States in the Puget lowlands, seriously limits natural regeneration. Without regeneration, opportunities for natural selection to favor alleles conferring genetic resistance or tolerance to blister rust are lost. This is especially unfortunate because *ex situ* collections from the Puget lowland are mostly lacking (Lipow et al. 2001). Given uncertainties about the distribution and frequency of valuable resistance alleles and expected ongoing population decline, additional gene conservation of western white pine in the Puget lowlands may be warranted. The ecoregion analysis, which suggested that a gap exists in the Puget lowlands, should be emphasized over the seed zone analysis since little information about patterns of genetic variation in the Puget lowlands is available (but see Steinhoff et al. 1983).

The gap analysis also draws attention to the fact western white pine is now extremely rare in the Oregon Coast Range. The only

remaining *in situ* western white pine germ plasm of Coast Range origin is found in a few small, natural stands on lands managed by the Oregon Department of Forestry and adjacent timberlands. The Oregon Department of Forestry has also created a few plantations with local seed and has a small clone bank (Alan Kanaskie, Oregon Department of Forestry, personal communication, 2005). These stands and plantations potentially contain unique genetic variation, and research designed to assess their genetic breadth and uniqueness would be desirable.

Efforts are under way to conserve the genetic resources of ponderosa pine in those areas where *in situ* protection is weakest. The US Army and The Nature Conservancy are working to conserve the only natural ponderosa pine stand in the Puget Sound area. An organization called the Willamette Valley Ponderosa Pine Conservation Association, formed in 1994, is working to protect the ponderosa pine in the Willamette Valley (McNitt 2001). The Association locates and maps remnant natural stands and collects and stores seed from them. They have established a seed orchard to ensure a

reliable source of seed with high genetic diversity and adaptability.

Forest managers of the Fremont National Forest are taking steps to guarantee the genetic integrity of ponderosa pine from the Oregon portion of the Warner Mountains. Ponderosa pine from this area is suspected of introgressing with Washoe pine, leading to genetically unique populations (Sorenson 1994; Paul Berrang, Fremont National Forest, personal communication, 2002), although there is some uncertainty about the relationship and genetic uniqueness of these taxa (Patten and Brunsfeld 2002). Forest managers have sufficient seed stored for use in replanting should a catastrophic fire strike. The remaining ponderosa pine strata that are not well protected are either the lowest or highest elevation bands in a seed zone, and their total acreage is small. In all cases, protection is adequate either in the next elevation band or in the same elevation band in a neighboring seed zone. This suggests that gene conservation measures may be desirable but are not of high priority at this time.

Regional genetic resources for western redcedar are particularly well conserved, with only three questionable strata. The Cowlitz/Chehalis foothills, Cowlitz/Newaukum prairie floodplains, and Fraser lowlands ecoregions have little protected area and appear as possible gaps for all analyzed species (see also Lipow et al. 2004). Because western redcedar displays atypically low genetic differentiation among populations (Copes 1981, Bower and Dunsworth 1988, Rehfeldt 1994, Yeh 1988), the seed zone analyses, which revealed no gaps, may be more appropriate than the ecoregion analyses. Therefore, further conservation of western redcedar in the three class 3 ecoregions is not a concern.

No critical gaps were found for western hemlock. In situ conservation is limited in the Cowlitz/Chehalis foothills, Cowlitz/Newaukum prairie floodplains, and Fraser Lowlands but is excellent in surrounding ecoregions. Genetic resources from the Cowlitz/Chehalis foothills and Cowlitz/Newaukum prairie floodplains are also safeguarded in ex situ progeny tests and breeding populations (Lipow et al. 2001). Although western hemlock has another gap in the Willamette Valley, the trees in Willamette Valley protected areas are expected to adequately sample and conserve the genetic resource. Finally, genetic resource conservation is good in ecoregions surrounding the Siskiyou foothills and in the Illinois and Rogue Valleys, which are the remaining class 3 strata for the species. These strata are arguably smaller than the area for which western hemlock populations display adaptation to local conditions (see Kuser and Ching 1980, Foster and Lester 1983).

Gap analysis appeared to be quite effective for evaluating the extent of in situ gene conservation for the forest trees studied. It enabled us to quantify the extent to which species are found and protected in regional ecoregions and seed zones and to display the results on maps, facilitating their interpretation and enabling easy comparisons among species. The results of this study should provide land managers in many areas with the assurance that the genetic resources for these important conifers are well protected in situ. The results also point to a few species and areas where additional conservation and research are warranted.

## Literature Cited

- BOWER, R.C., AND B.G. DUNSWORTH. 1988. Provenance test of western redcedar on Vancouver Island. P. 131–135 in *Proc. of conf. on Western redcedar—Does it have a future?*, Smith, N.J. (ed.). Univ. British Columbia, Vancouver, B.C., Canada.
- COPES, D.L. 1981. Isoenzyme uniformity in western redcedar seedlings from Oregon and Washington. *Can. J. For. Res.* 11:451–453.
- CRITCHFIELD, W.B., AND E.L. LITTLE JR. 1966. *Geographic distribution of the pines of the world*. USDA For. Serv. Misc. Pub. 991. 97 p.
- FOSTER, G.S., AND D.T. LESTER. 1983. Fifth-year height variation in western hemlock open-pollinated families growing on four test sites. *Can. J. For. Res.* 13:251–256.
- HALL, F.C. 1998. *Pacific Northwest ecoregion codes for seral and potential natural communities*. USDA For. Serv. Gen. Tech. Rep. PNW-GTR-418. 290 p.
- HAMRICK, J.L., M.J.W. GODT, AND S.L. SHERMAN-BROYLES. 1992. Factors influencing levels of genetic diversity in woody plant species. P. 95–124 in *Proc. of international symp. on population genetics of forest trees*, Adams, W.T., S.H. Strauss, and D.L. Copes, et al. (eds.). Kluwer Academic Publishers, Boston, MA.
- HENDERSON, J.A. 1997. *The PNV model*. USDA For. Serv. internal document. Mountlake Terrace, WA. 8 p.
- HENDERSON, J.A. 1998. *The USFS Potential Natural Vegetation Mapping Project*. 74 p.
- JOHNSON, M.D. 1998. *Region 6 inventory and monitoring system: Field procedures for the current vegetation survey, version 2.03. Natural resource inventory*. USDA Forest Service, Pacific Northwest Region, Portland, OR. Available online at [www.fs.fed.us/r6/survey/document.htm](http://www.fs.fed.us/r6/survey/document.htm); last accessed Feb. 2002.
- KILSGAARD, C. 1999. *Land cover type descriptions: Oregon gap analysis 1998 land cover for Oregon*. Oregon Natural Heritage Program, Portland, OR. 72 p.
- KUSER, J.E., AND K.K. CHING. 1980. Provenance variation in phenology and cold hardiness of western hemlock seedlings. *For. Sci.* 26:463–470.
- LIPOW, S.R., J.B. ST. CLAIR, AND G.R. JOHNSON. 2001. *Ex situ gene conservation for conifers in the Pacific Northwest*. USDA For. Serv. Gen. Tech. Rep. PNW-GTR-528. 54 p.
- LIPOW, S.R., K. VANCE-BORLAND, J.B. ST. CLAIR, J.A. HENDERSON, AND C. MCCAIN. 2004. Gap analysis of conserved genetic resources for forest trees. *Conserv. Biol.* 18:412–423.
- LYNCH, M. 1996. A quantitative-genetic perspective on conservation issues. P. 471–505 in *Conservation genetics: Case histories from nature*, Avise, J.C., and J.L. Hamrick (eds.). Chapman and Hall, New York, NY.
- MCCNITT, R.L. 2001. *Willamette Valley Ponderosa Pine Conservation Association home page*. Available online at [www.westernforestry.org/wvppca/](http://www.westernforestry.org/wvppca/); last accessed Oct. 2006.
- MONTREAL PROCESS. 1999. *Criteria and indicators for the conservation and sustainable management of temperate and boreal forests*, 2nd Ed. Montreal Process Liaison Office, Ottawa, Canada. Available online at [www.mpci.org/rep-pub/1999/ci\\_e.html](http://www.mpci.org/rep-pub/1999/ci_e.html).
- OMERNIK, J.M. 1995. Ecoregions: A spatial framework for environmental management. P. 49–62 in *Biological assessment and criteria: tools for water resource planning and decision making*, Davis, W.S., and T.P. Simon (eds.). Lewis Publishers, Boca Raton, FL.
- PATER, D.E., S.E. BRYCE, T.D. THORSON, J. KAGAN, C. CHAPPELL, J.M. OMERNIK, S.H. AZEVEDO, AND A.J. WOODS. 1998. *Ecoregions of western Washington and Oregon*. Map. Department of the Interior, US Geological Survey, Reston, VA.
- PATTEN, A.M., AND S.J. BRUNSFELD. 2002. Evidence of a novel lineage within the *Ponderosae*. *Madrono* 49:189–192.
- RANDALL, W.K. 1996. *Forest tree seed zones for western Oregon*. Oregon Department of Forestry, Salem, OR. 82 p.
- RANDALL, W.K. AND P. BERRANG. 2002. *Washington tree seed transfer zones*. Washington Department of Natural Resources, Olympia, WA. 81 p.
- REHFELDT, G.E. 1994. Genetic structure of western redcedar populations in the interior West. *Can. J. For. Res.* 24:670–680.
- SCOTT, J.M., AND M.D. JENNINGS. 1997. *A description of the national gap analysis program*. Available online at [www.gap.uidaho.edu/About/Overview/GapDescription/default.htm](http://www.gap.uidaho.edu/About/Overview/GapDescription/default.htm); last accessed Oct. 2003.
- SCOTT, J.M., AND M.D. JENNINGS. 1998. Large-area mapping of biodiversity. *Ann. Missouri Bot. Gard.* 85:34–47.
- SORENSEN, F.C. 1994. *Geographic variation and seed transfer guidelines for ponderosa pine in central Oregon*. USDA For. Serv. Pacific Northwest Research Station Res. Pap. PNW-RP-472. 24 p.
- STEINHOFF, R.L., D.G. JOYCE, AND L. FINS. 1983. Isozyme variation in *Pinus monticola*. *Can. J. For. Res.* 13:1122–1132.
- YANCHUK, A.D. 2001. A quantitative framework for breeding and conservation of forest tree genetic resources in British Columbia. *Can. J. For. Res.* 31:566–576.
- YANCHUK, A.D., AND D.T. LESTER. 1996. Setting priorities for conservation of the conifer genetic resources of British Columbia. *For. Chron.* 72:406–415.
- YEH, F.C. 1988. Isozyme variation of *Thuja plicata* (Cupressaceae) in British Columbia. *Biochem. Systematics Ecol.* 16:373–377.